ENVIRONMENTAL COVARIATES OF SABLEFISH (ANOPLOPOMA FIMBRIA) AND PACIFIC OCEAN PERCH (SEBASTES ALUTUS) RECRUITMENT IN THE GULF OF ALASKA

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Abstract

The sablefish (*Anoplopoma fimbria*) and Pacific ocean perch (POP; *Sebastes alutus*) fisheries in the Gulf of Alaska (GOA) are both highly lucrative and variable. Determining environmental factors that drive variability in year class strength may improve their forecasts, leading to more effective management. Here we examine relationships between sablefish and POP recruitment and multiple environmental indices associated with circulation in the GOA. We used hierarchical cluster analysis to determine spatially and seasonally relevant scales for analyzing these relationships, a relatively novel approach that may be of use to similar studies. We used structural equation modeling to examine sequential relationships between large-scale climate variables, regional (eastern and western GOA) environmental variables, and recruitment using both hypothesis-testing and exploratory approaches. Exploratory analyses revealed that sablefish recruitment was positively related to July upwelling-favorable winds and negatively related to late winter freshwater discharge in the eastern gulf during age 1. POP recruitment was negatively related to June upwelling-favorable winds in both regions during ages 0 and 1 and positively related to late spring freshwater discharge during age 1. These results suggest that upwelling-favorable winds and freshwater discharge may affect recruitment of both species through productivity-related mechanisms, and may additionally affect POP recruitment through advection-related mechanisms. Targeted studies at the appropriate scales are needed to provide greater certainty in the potential mechanisms behind these relationships.

Table of Contents

List of Figures

List of Tables

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Introduction

The Gulf of Alaska (GOA) supports some of Alaska's most highly productive fisheries, with commercial yields often exceeding 200,000 tons during recent years (Fissel et al., 2012). Many commercially important fish species in this region have highly variable recruitment, which can make it difficult to estimate biological reference points that allow for efficient utilization of these fisheries. Several species in the GOA, including sablefish (*Anoplopoma fimbria*) and Pacific ocean perch (POP; *Sebastes alutus*), spawn offshore near the continental slope and rely on nearshore nursery habitats during their early life history (Paraketsov, 1963; Carlson and Haight, 1976; Sasaki, 1985; Rutecki and Varosi, 1997b; Rooper et al., 2007; Bailey et al., 2008). For these species, variability in recruitment is thought to be driven largely by environmental factors affecting their larval survival while advected across the continental shelf.

One of the primary goals of the Gulf of Alaska Integrated Ecosystem Research Project (GOA IERP) is to identify specific factors that may influence the survival of commercially important groundfish as they make their passage across the GOA shelf, focusing on five key species: sablefish, POP, walleye pollock (*Gadus chalcogrammus*), Pacific cod (*Gadus macrocephalus*), and arrowtooth flounder (*Atheresthes stomias*) (NPRB, 2011). One of the objectives of this project is to identify the effects of environmental variability in the GOA on recruitment of these five species (NPRB, 2011). This study aims to contribute to this objective through a retrospective analysis of climate and oceanographic features that may relate to the advection of larval sablefish and POP towards their nearshore nursery habitats.

Sablefish in Alaska are managed as a single population due to their high rates of migration throughout Alaskan waters (Heifetz and Fujioka, 1991; Hanselman et al., 2011). spawn in deep waters along the continental slope during spring, with a peak spawning date

during February – March (Wing and Kamikawa, 1995; Wing, 1997). Their eggs hatch after several weeks, and larvae immediately swim to the surface and begin drifting towards nearshore nursery areas, which they reach during summer and fall (Rutecki and Varosi, 1997a, b).

POP in the GOA maintain fertilized eggs internally until they hatch; larval parturition occurs during April and May in deep waters along the slope, as well as in canyons and gullies (Paraketsov, 1963; Gunderson, 1971, 1972; Rooper et al., 2007). Their larvae remain planktic near the ocean surface for an unknown time period before reaching their nearshore nursery grounds (Carlson and Haight, 1976; Rooper et al., 2007). The population structure of POP in the GOA consists of multiple genetically distinct subpopulations, which indicates that dispersal is geographically limited throughout their life history (Palof et al., 2011; Kamin et al., 2013).

Two primary oceanographic features in the GOA are the Subarctic Gyre and the Alaska Coastal Current (ACC); the former is wind-driven while the latter is driven by a combination of winds and freshwater discharge (Royer, 1982; Stabeno et al., 2004). The circulation patterns associated with these oceanographic features result in generally downwelling-favorable conditions along the GOA coastline (Stabeno et al., 2004), though episodic upwelling occurs during spring and summer.

We[1] propose that recruitment of sablefish and POP may be enhanced if strong downwelling conditions advect their larvae more quickly towards nearshore nursery sites. Conversely, high freshwater discharge during this time period may be detrimental to their recruitment, as a more intense ACC may create a front that acts as a physical barrier between larvae in offshore waters and their nearshore nursery sites or may advect larvae downstream and away from suitable sites.

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Freshwater discharge and downwelling in the GOA are associated with large-scale climate and oceanographic patterns reflected by indices, such as the Pacific Decadal Oscillation (PDO; Mantua et al., 1997), the Northern Oscillation Index (NOI; Schwing et al., 2002), and the North Pacific Gyre Oscillation (NPGO; Di Lorenzo et al., 2008). Conditions indicated by these climate variables may indirectly affect recruitment of sablefish and POP through their influence on regional downwelling strength and freshwater discharge; furthermore, circulation conditions associated with the NPGO may directly affect recruitment of POP by dispersing larvae away from suitable habitat.

The overall goal of this thesis is to investigate sequential relationships between climate variables, regional variables, and recruitment of sablefish and POP in the GOA using confirmatory and exploratory structural modeling approaches. I hope to accomplish this by answering the following questions:

1. Is there a sequential relationship between winter PDO or NOI, spring downwelling strength in the GOA, and recruitment of sablefish or POP?
2. Is there a sequential relationship between winter PDO, summer freshwater discharge in the GOA, and recruitment of sablefish or POP?
3. Is POP recruitment negatively related to the NPGO?

Background

Sablefish (*Anoplopoma fimbria*) and Pacific ocean perch (POP, *Sebastes alutus*) both support highly lucrative commercial fisheries in the Gulf of Alaska (GOA). Improved management of these fisheries, including more accurate recruitment forecasts in stock assessments, can help make them more efficient and thus more profitable while lowering the risk of overfishing (Haddon, 2001). Incorporating influential environmental variables at appropriate geographic scales into stock assessment models can contribute towards improving forecast accuracy, particularly for species without established stock-recruit relationships (Haddon, 2001; Deriso et al., 2008; Shotwell et al., 2014). This study seeks to determine potential relationships of several specific climate and regional-scale environmental processes (as revealed by derived indices) to sablefish and POP recruitment in the GOA, as well as to identify the specific regions that exhibit the strongest recruitment-environment relationships.

Sablefish

Fishery

Sablefish are one of the most commercially important fisheries in Alaska, with annual ex-vessel values ranging from US $85 million to US $143 million between 2007 and 2011 (Fissel et al., 2012). The sablefish stock assessment (Hanselman et al., 2011a) contains a review of this fishery's history: it was primarily exploited by the United States and Canada until the late 1950s, when Japanese longliners began expanding through the Bering Sea and GOA. Foreign fisheries, including Japan, Russia, and Korea, continued to dominate the sablefish fishing effort in Alaskan waters until the 1980s, with particularly heavy fishing during the 1970s. Catch peaked at over

53,100 t in 1972 and declined through the late 1970s due to population declines and the establishment of the Fishery Conservation and Management Act of 1976. The Alaskan sablefish fishery was domesticated in the 1980s, and catches increased again until they reached another peak in 1988 (about 38,400 t); since then, abundance has remained relatively low, averaging around 12,000 t in recent years. The sablefish fishery is primarily prosecuted as a longline fishery, though the use of pot gear has increased in recent years as a response to whale depredation. Individual Fishing Quota (IFQ) management was established for Alaskan sablefish in 1995, and quotas are allocated by gear type and region.

Effective management is necessary to ensure optimum yield and continued profitability for this fishery. Incorporating relevant environmental variables into stock assessment models may improve year-class strength (YCS) predictions, which allows for more accurate predictions of future biomass and biological reference points, reducing the risk of overfishing and underutilization (Haddon, 2001; Deriso et al., 2008; Shotwell et al., 2014). For sablefish, variability in YCS is likely heavily influenced by factors affecting survival during their early life history, about which little is known.

Biology

Sablefish are a deep-sea fish inhabiting the North Pacific, with a southern range limit extending to Sagami Bay, Japan, in the western Pacific to Baja California, Mexico, in the eastern Pacific (Sasaki, 1985; Wolotira et al., 1993). Sablefish in federal waters off Alaska are managed as a single stock due to their widespread migration within this region (Heifetz and Fujioka, 1991; Kimura et al., 1998; Hanselman et al., 2011a). Sablefish in British Colombia spawn offshore at depths of 300 – 500 m during spring (Mason et al., 1983). Based on studies on their larval

distribution, Alaskan sablefish are also believed to spawn offshore at similar depths, with an approximate peak spawning date during February – March (Wing and Kamikawa, 1995; Wing, 1997). While there is little information on the incubation time and depth of Alaskan sablefish eggs, studies on other stocks indicate that their eggs incubate for several weeks, during which time they increase in density and sink to depths of 400 – 1000 m before hatching (Mason et al., 1983; Kendall and Matarese, 1987). Newly hatched larvae move to the surface and remain neustonic as they drift towards nearshore waters, which serve as important nursery habitat (Sasaki, 1985; Kendall and Matarese, 1987; Rutecki and Varosi, 1997b; Wing, 1997). Alaskan young-of-year sablefish are believed to reach the nearshore and settle during summer and fall (Rutecki and Varosi, 1997a, b); juveniles remain in these nearshore nursery sites until roughly age 2, at which point they migrate back offshore (Rutecki and Varosi, 1997b; Maloney and Sigler, 2008). They reach their adult habitat and recruit to the fishery at around age 4 (Maloney and Sigler, 2008).

Pacific ocean perch

Fishery

POP comprise the majority of commercial rockfish catch in the GOA, which had an ex-vessel value ranging from US $5.1 million to US $9.1 million between 2007 and 2011 (Hanselman et al., 2011b; Fissel et al., 2012). The POP stock assessment (Hanselman et al. 2011b) contains a review of the POP fishery: it was primarily prosecuted by Japan and the USSR from the 1960s until the 1980s, when the domestic fishery began expanding. POP were overfished during the 1960s, when annual catch peaked at 350,000 t in 1965 and decreased

throughout the rest of the 1960s through the early 1980s. Catches increased somewhat after reaching a minimum in 1985, but remained low through the mid-1990s due to restrictive management measures, including total allowable catch (TAC) reductions meant to help rebuild stocks. Since the late 1990s, catch has increased and has remained near 13,000 t in recent years. The POP fishery in the GOA is primarily prosecuted as a bottom trawl fishery, though pelagic trawls have increased in recent years as smaller catcher vessels comprise an increasing portion of the fishery. As with sablefish, POP fishery management may benefit from incorporating environmental variables that reflect conditions affecting survival during their early life history if those variables improve recruitment forecasts.

Biology

POP inhabit demersal shelf and slope habitat throughout the North Pacific, but catches are most abundant in the GOA and Aleutian Islands (Carlson and Haight, 1976; Allen and Smith, 1988). POP in the GOA consist of genetically distinct subpopulations that occur at small geographic scales, indicating that larval dispersal is limited (Palof et al., 2011; Kamin et al., 2013). Female POP are ovoviviparous, maintaining fertilized eggs internally until hatching and larval parturition (Gunderson, 1971). They spawn during the fall, and parturition occurs during April and May in gullies, canyons, and along the slope at depths of 500 – 700 m (Paraketsov, 1963; Gunderson, 1971, 1972; Rooper et al., 2007). Larvae remain planktic near the ocean surface for an unknown time period before settling in their demersal nearshore nursery habitat, which consists of rough substrata and complex structure comprised of boulders, corals, and sponges (Carlson and Haight, 1976; Rooper et al., 2007). They remain in their nursery habitat until roughly age 3, at which point they begin to migrate offshore towards their adult habitat

(Carlson and Haight, 1976; Carlson and Straty, 1981). They reach their adult habitat in gullies and along the continental slope by age 6 (Carlson and Haight, 1976; Gunderson, 1977).

Study Area

The GOA continental shelf varies in width from 5 km to 200 km, being generally narrower in the eastern GOA and broader to the west (Weingartner, 2007). Depth on the shelf predominantly ranges over 150 m to 200 m, and the shelf-break occurs at a depth of 200 – 300 m (Weingartner, 2007). Bathymetry on the GOA shelf is highly complex, including many cross-shelf canyons and gullies, due to millennia of heavy tectonic and glacial activity; these canyons and gullies may serve as major pathways for the exchange of water masses and associated nutrients and organisms between the shelf and basin (Weingartner, 2007).

Ocean circulation in the GOA is primarily influenced by two main current systems: the Subarctic Gyre over the slope and basin and the Alaska Coastal Current (ACC) along the coast (Fig. 1; Stabeno et al., 2004). The Subarctic Gyre system is comprised of three currents that combine to create a cyclonic circulation pattern: the North Pacific Current, the Alaska Current, and the Alaskan Stream (Stabeno et al., 2004). Transport of water in this current system is mostly driven by cyclonic winds, which are associated with downwelling-favorable conditions along Alaska's southern coastline (Stabeno et al., 2004). During spring and summer months, these downwelling conditions weaken and are accompanied by intermittent and variable upwelling events (Stabeno et al., 2004).

The ACC flows counter-clockwise along the GOA coastline before flowing into the Bering Sea through the Aleutian passes, and is driven by a combination of alongshore winds and freshwater discharge into the GOA (Royer, 1982; Stabeno et al., 2004; Weingartner et al., 2005).

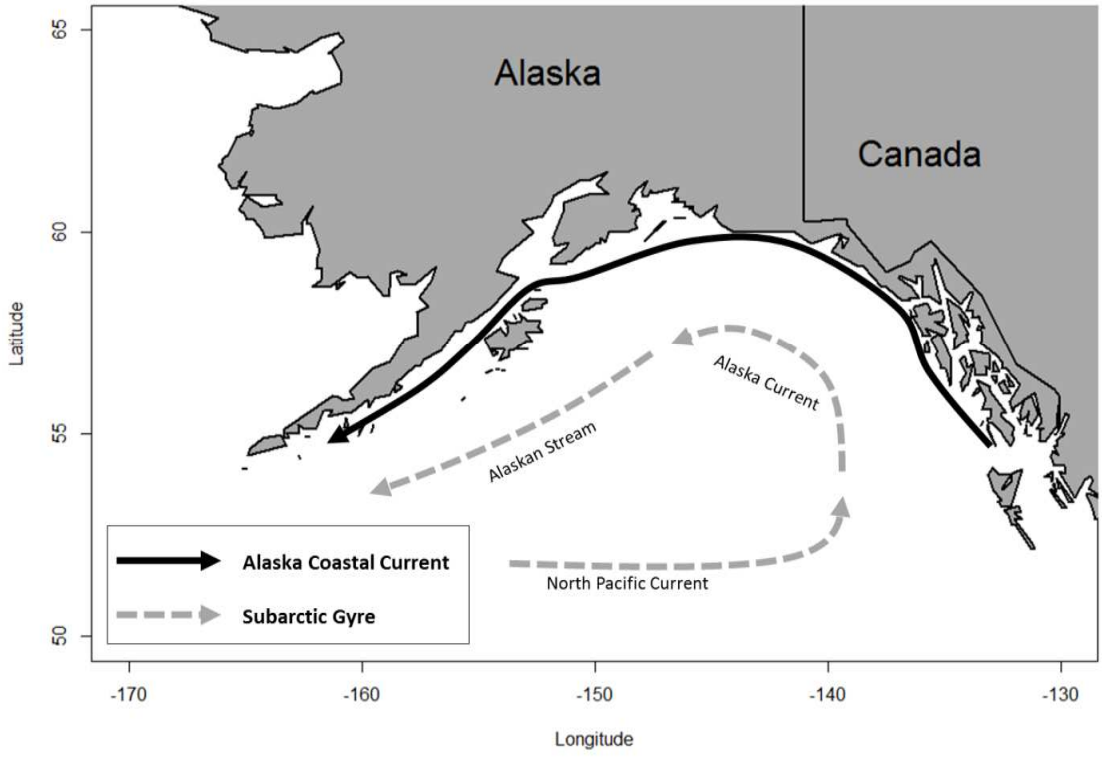

Figure 1. Gulf of Alaska (GOA) currents. Current systems driving circulation in the GOA.

The prominence of its freshwater core is reduced during spring and summer as water spreads offshore due to relaxed downwelling or upwelling (Stabeno et al., 2004).

Regional environmental conditions in the GOA may be related on interannual time scales to large-scale climate oscillations, including those indexed by the Northern Oscillation Index (NOI; Schwing et al., 2002), the North Pacific Gyre Oscillation (NPGO; Di Lorenzo et al., 2008), and the Pacific Decadal Oscillation (PDO; Mantua et al., 1997). The NOI is based on differences in sea level pressure anomalies (SLPa) between the North Pacific High (NPH) and a low-pressure region near Darwin, Australia (Schwing et al., 2002), thus incorporating both tropical and extratropical variations in climate. The NOI is dominated by similar variations to those associated with El Niño-Southern Oscillation (ENSO), with which it shares a strong negative correlation (Schwing et al., 2002). Greater differences in SLPa between the NPH and Darwin, Australia result in stronger, easterly-flowing trade winds, strengthening Hadley-Walker circulation between the two regions (Schwing et al., 2002). This creates greater anticyclonic surface wind stresses in the northeast Pacific, resulting in greater upwelling at the coast and cooler sea surface temperatures (SST) in the northeast Pacific (Schwing et al., 2002). In the GOA, positive NOI values reflect lower sea level pressure towards the east, higher sea level pressure towards the west, cooler SST, and stronger upwelling-favorable winds (Schwing et al., 2002).

The NPGO is defined as the 2nd principal component of variability in sea surface height anomalies in the northeast Pacific Ocean (Di Lorenzo et al., 2008). This index reflects changes in wind-stress throughout this region, and is significantly correlated with anomalies in sea surface salinity, surface chlorophyll-*a* concentration, and nutrient concentrations (Di Lorenzo et al., 2008). During a positive NPGO phase, the Subarctic Gyre shifts farther north and

geostrophic circulation in the northeast Pacific is generally intensified, resulting in increased transport in both the ACC and the California Current System (Di Lorenzo et al., 2008). These conditions are associated with increased coastal upwelling, greater nutrient concentrations, greater sea surface salinity, and increased primary productivity in the California Current region; in the GOA, these conditions are associated with stronger downwelling in coastal waters and stronger upwelling within the Subarctic Gyre (Di Lorenzo et al., 2008).

The PDO is defined as the leading principal component of sea surface temperature variability in the North Pacific (Mantua et al., 1997). The forcing mechanisms behind the PDO are uncertain, but some evidence suggests that these include ENSO, circulation anomalies in the Kuroshio-Oyashio Extension Region, and the location and intensity of the Aleutian Low (Mantua et al., 1997; Bond et al., 2003; Rodionov et al., 2005; Schneider and Cornuelle, 2005; Chhak et al., 2009; Di Lorenzo et al., 2013). During a positive PDO phase, the Aleutian Low is intensified and its location shifts farther east, resulting in lower pressures and enhanced cyclonic winds over the North Pacific (Trenberth, 1990; Trenberth and Hurrell, 1994; Mantua et al., 1997). These cyclonic winds enhance the flow of warm, moist air along the south Alaskan coast, leading to increased precipitation and freshwater discharge (Cayan and Peterson, 1989; Trenberth, 1990; Mantua et al., 1997). Additionally, this wind stress pattern enhances anticyclonic circulation in North Pacific waters, resulting in warmer coastal SST, enhanced upwelling in the center of the Subarctic Gyre, and lower flow of water entering the California Current System (Trenberth, 1990; Salmon, 1992; Trenberth and Hurrell, 1994). Thus, positive PDO values reflect enhanced downwelling-favorable winds, warmer sea surface temperatures, and greater precipitation in the GOA (Cayan and Peterson, 1989; Trenberth, 1990; Salmon, 1992; Trenberth and Hurrell, 1994; Mantua et al., 1997).

Goals and rationale

Sablefish and POP recruitment in Alaska both have very high interannual variability (Fig. 2). Estimated YCS at age 0 for sablefish ranges from less than 1 million recruits in 1983 and 1990 to approximately 95 million in 1960 (Hanselman et al., 2011a). For POP, YCS at age 0 ranges from approximately 18 million recruits in 1975 to nearly 229 million in 1986 (Hanselman et al., 2011b). No reliable stock-recruit relationships have been identified for either species, suggesting that environmental factors play a dominant role in determining their YCS (Hanselman et al., 2011a; Hanselman et al., 2011b; Shotwell et al., 2014). Sablefish recruitment in the North Pacific has been linked to several large-scale climate and oceanographic features, including the PDO, the Aleutian Low, and the North Pacific Polar Front (McFarlane and Beamish, 1992; Hare and Mantua, 2000; King et al., 2000; Sogard, 2011; Shotwell et al., 2014). However, relationships between either species' recruitment and regional-scale environmental indices remain largely unexplored, and may contribute insight into the mechanisms linking recruitment to large-scale oceanographic features (Shotwell et al., 2014).

One potentially important factor affecting variability in the recruitment of slope-spawning species, such as sablefish and POP, is their need to cross the shelf to reach nearshore nursery habitats after hatching. There are several proposed mechanisms of cross-shelf advection for other GOA groundfish species (e.g., flatfish) during their larval phase, including onshore advection in deep waters during upwelling and relaxed downwelling for species occurring deeper in the water column, propagation of retention features such as eddies, bathymetric steering at depth, and shoreward advection at the surface during downwelling-favorable conditions (Weingartner, 2007; Bailey et al., 2008). While mechanisms operating at depth are unlikely to

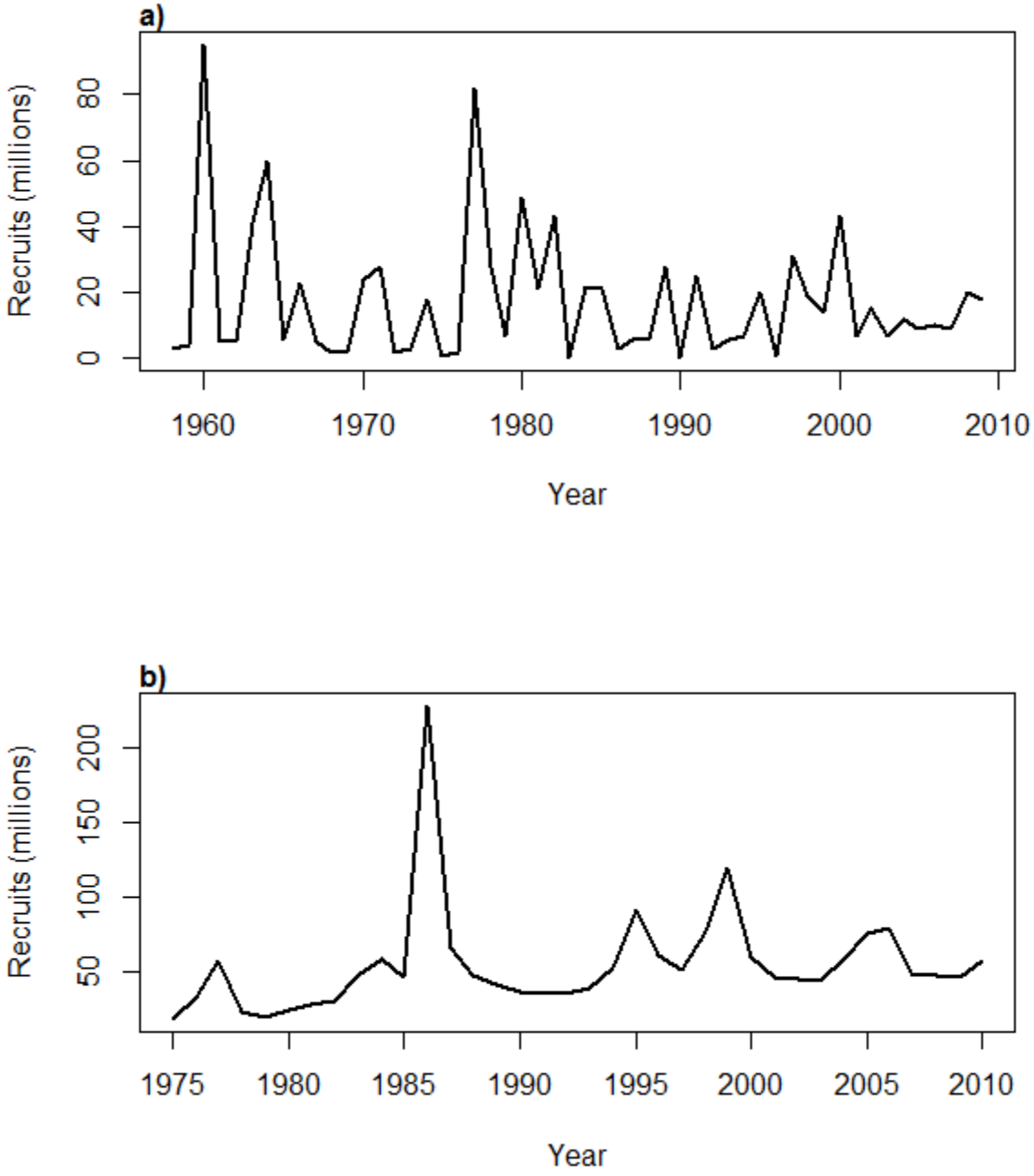

Figure 2. Year class strengths. Time series of estimated year class strength of (a) sablefish over 1958 – 2009 and (b) POP over 1975 – 2010.

apply to sablefish or POP larvae, it is likely that the cyclonic currents and wind conditions in the GOA influence larval advection of both species across the shelf to their juvenile nursery habitats, as they do for other deep-spawning fish species in Alaska (e.g., Bailey et al., 2008; Doyle et al., 2009). Sablefish recruitment for the United States west coast stock has been linked to timing of spring transition in the California current system, with earlier shifts towards upwelling-favorable southward flow resulting in greater year-class strength (Schirripa and Colbert, 2006). However, this relationship applied to upwelling during months after larval sablefish had reached their nearshore nursery habitat, and the relationship was attributed largely to the effect of upwelling on juvenile sablefish prey condition and abundance (Schirripa and Colbert, 2006). Such relationships between downwelling conditions, physical advection, and recruitment have not been rigorously evaluated for sablefish or POP in the GOA.

The main goal of this study is to investigate potential relationships between large-scale climate variables (indicated by the PDO, the NPGO, and the NOI), regional environmental variables (indicated by downwelling and freshwater discharge indices), and recruitment of sablefish and POP in the GOA. We focus on downwelling and freshwater discharge because cross-shelf transport of larvae at the surface is likely to be strongly affected by surface Ekman transport and alongshelf currents. Specifically, we propose that their recruitment may be enhanced if shoreward advection is increased by strong downwelling conditions during the period of larval drift. If this is the case, recruitment of both species may show a positive relationship to downwelling strength during this time. A strong ACC, in contrast, may act as a barrier to shoreward advection when coupled with downwelling conditions that intensify the front between this freshwater-core current and surrounding seawater, and may therefore weaken recruitment if larvae are lost through alongshore advection towards unfavorable areas. Finally,

given that the population structure of POP suggests limited lifetime dispersal, enhanced alongshore transport may reduce their larval survival and subsequent recruitment through enhanced advection towards unfavorable habitat.

Our climate indices were chosen primarily based on their relationships to oceanographic circulation in the GOA. The NOI contains information on forcing mechanisms operating across both the northeast and tropical Pacific regions (Schwing et al., 2002). While it is strongly related to the ENSO index, the NOI is based on the NPH and has a more direct relationship with processes operating at high northern latitudes, making it more suitable for investigating relationships between physical forcing and biological responses in the northeast Pacific (Schwing et al., 2002). Therefore, this index was chosen over ENSO as an indicator of climate conditions associated with downwelling conditions along the GOA coast.

The association between the NPGO and wind stress in the northeast Pacific makes this index useful for describing variability in the gyre circulation throughout the GOA. Although it is more strongly associated with coastal upwelling and downwelling south of 38° N, the relationship between the NPGO and the strength of the Subarctic Gyre make it potentially useful for testing relationships between alongshelf advection and recruitment in the GOA. Furthermore, given its correlation with primary productivity in the northeast Pacific, the NPGO index may be useful for exploring ecological forcing mechanisms beyond those related to circulation (Di Lorenzo et al., 2008).

The PDO is associated with both downwelling and freshwater discharge in the GOA. Specifically, the index is highly correlated with coastal upwelling and downwelling at latitudes north of 38° N (Mantua et al., 1997), making it a useful complement to the NPGO when examining temporal downwelling variability in the northeast Pacific. In addition, the PDO is

linked to variability in coastal temperatures, which affect the amount of precipitation and the melt-freeze cycle and therefore the amount and timing of freshwater discharge (Royer, 1982; Mantua et al., 1997; Royer and Grosch, 2006). While each of these three climate indices is associated with winds and circulation in the northeast Pacific, weak to moderate correlations among the indices suggest that each captures unique aspects of the variability in circulation and transport in the GOA; therefore we included all three indices in the analysis. The NOI oscillates at shorter interannual time scales than the other two indices, which operate on interdecadal time scales; furthermore, the NPGO and the PDO are statistically independent of each other and thus relate to different sources of variability in winds and circulation (Mantua et al., 1997; Schwing et al., 2002; Di Lorenzo et al., 2008; Chhak et al., 2009).

We further propose that conditions in the eastern (E) GOA may have a more significant impact on recruitment than conditions in the western (W) GOA, especially for sablefish. Regional variability in downwelling and freshwater discharge may have different effects on total recruitment of both species due to the broader continental shelf in the W GOA (Weingartner et al., 2002; Weingartner et al., 2009), which may provide a greater challenge to shoreward advection of larvae spawned in this region due to the greater distance required to travel from shelf-break to shore. Additionally, it has been proposed that most sablefish spawning likely occurs in the E GOA (Heifetz and Fujioka, 1991; Wing and Kamikawa, 1995; Sigler et al., 2001; Maloney and Sigler, 2008). Therefore, we examined downwelling-favorable winds and freshwater discharge separately for each region of the GOA and used regional-scale indices in addition to large-scale climate indices in our analysis.

Methods

We used a structural equation modeling (SEM; Bollen, 1989) approach to examine sequential relationships between recruitment, regional environmental variables, and large-scale climate variables at different seasonal lags. SEM is a confirmatory modeling technique that allows simultaneous testing of multiple hypothesized relationships, referred to as "paths" in SEM, between variables as separate steps within a complex model (Bollen, 1989; Ullman et al., 2007; Grace et al., 2010). Each path leads from an exogenous (explanatory) variable to an endogenous (response) variable; variables fulfilling both roles (i.e., those occupying the middle step within the model) are often referred to as "intermediary" variables (Bollen, 1989; Ullman et al., 2007; Grace et al., 2010). The use of multiple paths within a model makes SEM a useful technique for evaluating hypotheses that propose a sequential series of causal effects between variables (Grace et al., 2010). This approach has been used in other studies to investigate sequences between large-scale climate variables, regional variables, and fish recruitment (e.g., Fukuwaka et al., 2011), and we used it similarly here.

Data

We compiled monthly or annual time series of biological (response) and physical (explanatory) variables spanning at least three decades (Table 1; Fig. 3). The abundances of recruits for each species were obtained from an age-structured model that is used in each species' stock assessment (Hanselman et al., 2011a; Hanselman et al., 2011b). The model is fit to abundance indices from trawl and longline surveys, as well as to age- and length-composition data from the surveys and from the fishery, in order to estimate spawning biomass, fishing mortality, and abundance of recruits at age-2. Recruit abundance is estimated at age-2 because

Table 1 Variables used in analyses: Sources, timespans, and resolutions of time series used in analyses.

Variable	Source	Time Period	Spatial Resolution	Temporal Resolution
Sablefish age 2 recruit abundance	Hanselman et al. (2011a)	1960 - 2011	Alaskan waters	Annual
Sablefish spawning biomass	Hanselman et al. (2011a)	1960 - 2011	Alaskan waters	Annual
POP age 2 recruit abundance	Hanselman et al. (2011b)	1977 - 2011	Gulfwide	Annual
POP spawning biomass	Hanselman et al. (2011b)	1977 - 2011	Gulfwide	Annual
Freshwater discharge	University of Alaska Fairbanks Institute of Marine Science (IMS) http://www.ims.uaf.edu/gak1/	1931 - 2011	Eastern GOA, central GOA, and total	Monthly
Upwelling-favorable winds	Pacific Fisheries Environmental Laboratory (PFEL) http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/upwelling.html	1967 - 2011	1-degree grid	6-hourly
Pacific Decadal Oscillation (PDO)	University of Washington Joint Institute for the Study of the Atmosphere and Ocean (JISAO) http://jisao.washington.edu/data_sets/pdo/	1900 - 2012	North Pacific Ocean	Monthly
Northern Oscillation Index (NOI)	Pacific Fisheries Environmental Laboratory (PFEL) http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/NOIx/noix.html	1948 - 2012	North Pacific Ocean	Monthly

Table 1 (continued)

Variable	Source	Time Period	Spatial Resolution	Temporal Resolution
North Pacific Gyre Oscillation (NPGO)	Georgia Institute of Technology School of Earth & Atmospheric Sciences (EAS) http://www.o3d.org/npgo/	1950 - 2010	North Pacific Ocean	Monthly

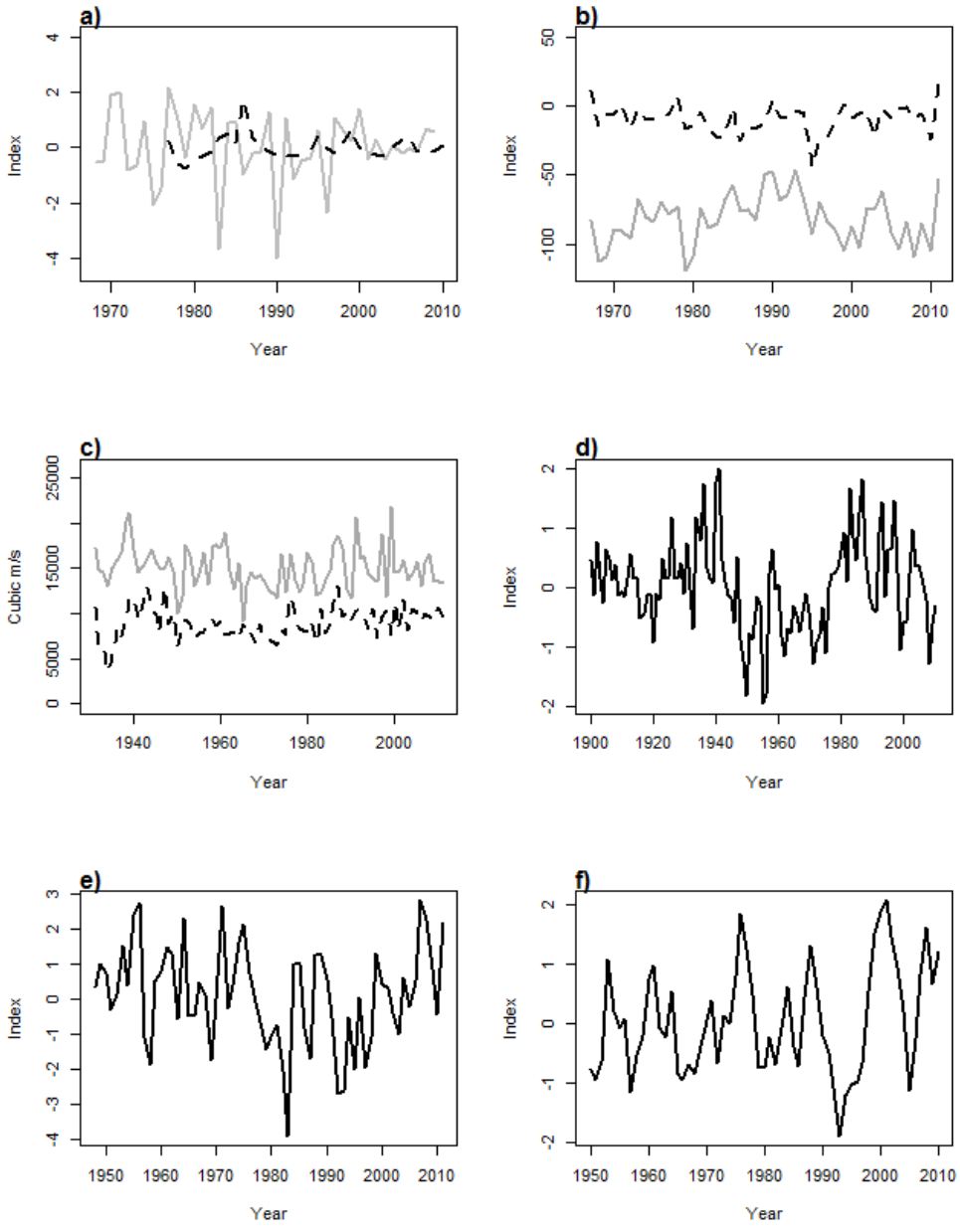

Figure 3. Variable time series. Annual time series of variables used in analysis. Panels refer to (a) recruitment (Ricker model residuals), (b) upwelling-favorable winds, (c) freshwater discharge, (d) PDO, (e) NOI, and (f) NPGO. For recruitment (a), the solid line represents sablefish (years 1968 – 2009) and the dotted line represents POP (years 1977 – 2010). For upwelling-favorable winds (b) and discharge (c), solid lines represent the eastern GOA while dotted lines represent the western GOA (central GOA for freshwater discharge).

the traditional adult surveys do not select for younger ages and data on earlier life history stages are incongruent (Hanselman et al., 2011a; Hanselman et al., 2011b; Shotwell et al., 2014).

The assessment model is then used to project future biomass trends under different harvest scenarios as a basis for recommending an acceptable biological catch (ABC; Hanselman et al., 2011a; Hanselman et al., 2011b; Shotwell et al., 2014). Due to the lack of clear spawner-recruit relationships for sablefish or POP, future recruit abundances for the projections are simulated to mimic the distribution of historical recruit abundances. For each year of the projections, numbers at age (including the simulated number at age 2) are projected forward using estimates of natural mortality, selectivity, and fishing mortality (under the pre-determined harvest scenario). These projections are repeated for each of several alternate harvest scenarios ranging from no harvest to maximum ABC to determine stock status (Hanselman et al., 2011a; Hanselman et al., 2011b).

Although there is little evidence for a stock-recruitment relationship in these species and uncertainty about its functional form (Fig. 4; Hanselman et al., 2011a; Hanselman et al., 2011b), we considered it prudent to remove potential density-dependence prior to analysis. To adjust for potential effects of spawner abundance on recruitment, we fit a Ricker model for each species as follows:

$$\log\left(R_{t+2}/S_t\right) = \alpha + \beta\, S_t + \varepsilon_t, \qquad [1]$$

where R_{t+2} denotes age 2 recruit abundance in year $t+2$, S_t denotes spawning biomass in year t, α and β denote the productivity and carrying capacity parameters of the Ricker stock-recruitment relationship, and ε_t denotes residual errors. The time series of residuals from each Ricker model were used as the response variable (hereafter referred to as "recruitment") in all SEM analyses as

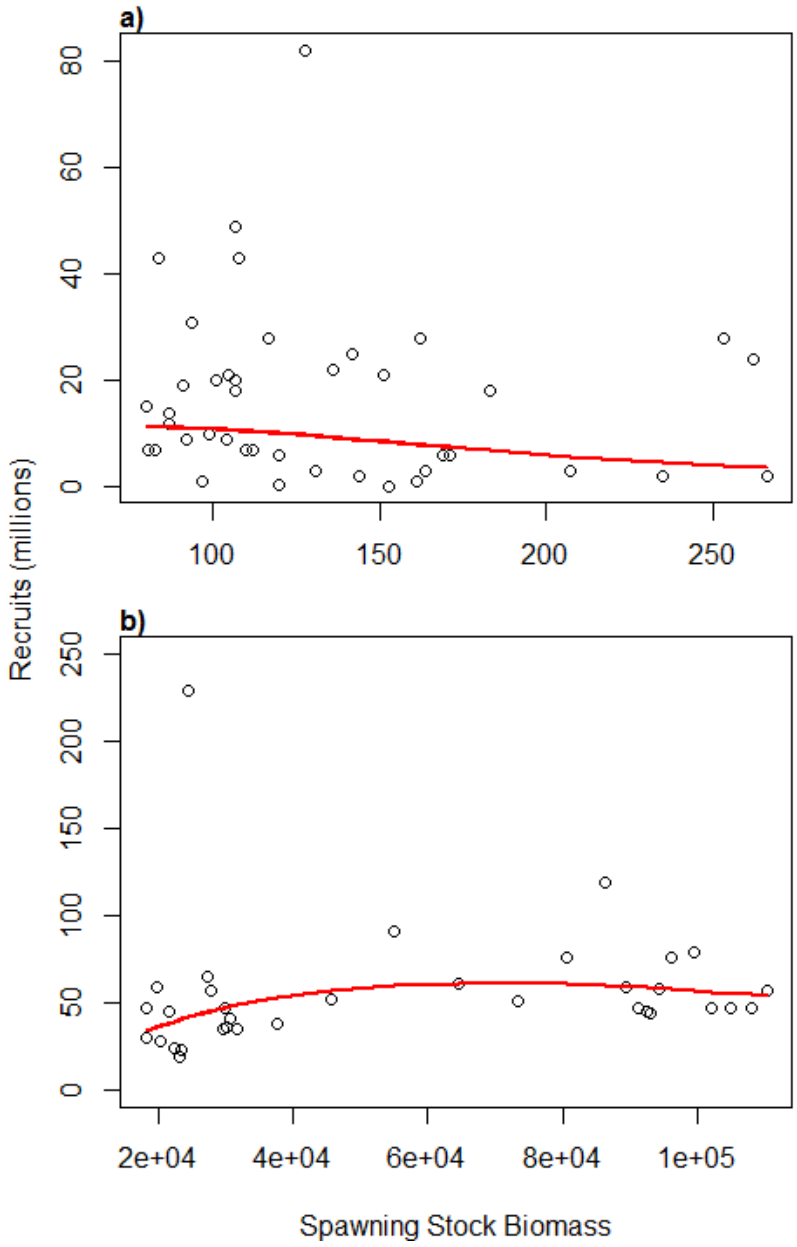

Figure 4. Spawner-recruit relationships. Spawner-recruit relationships for sablefish (a) and POP (b). Lines represent fitted values from Ricker models.

a measure of anomalies in (log-transformed) survival from spawning to recruitment. Repeating the analyses with log-transformed raw recruitment time series did not affect our overall conclusions, indicating that results are robust to the nature of the stock-recruitment relationship. This was expected given that the log-transformed recruit abundance and Ricker model residual time series were highly correlated for both sablefish ($r = 0.97$; $p < 0.001$) and POP ($r = 0.92$; $p < 0.001$).

For each environmental variable, the full time series (Table 1) was used to elucidate seasonal and spatial patterns. For use in the SEM analysis, time series were truncated to only include years that had data for all variables (1977 – 2010 for POP; 1968 – 2009 for sablefish). Monthly freshwater discharge estimates (m^3s^{-1}) are based on a model incorporating precipitation, air temperature, and glacial melt (Royer, 1982; Royer and Grosch, 2006). These estimates are provided for two coastal drainage regions: discharge in the eastern (E) GOA (east of Yakutat) was used to characterize variability in the ACC in southeast Alaska, while discharge in the central (C) GOA (Seward to Yakutat) was used as a separate index to characterize variability in the central transition region where the ACC is highly complex (Royer, 1982, Stabeno et al. 2004). A combined index ("total discharge") consisting of the sum of E GOA discharge in a given month plus C GOA discharge in the following month provides a measure of variability in the total volume flow of the ACC in the western (W) GOA downstream of Seward, or west of ~149.4˚W (Royer, 1982; Weingartner et al., 2005). Although the three indices are moderately to highly correlated (E GOA vs C GOA: $r = 0.66$; E GOA vs total: $r = 0.74$; C GOA vs. W GOA: $r = 0.74$; all $p < 0.001$), we used all three indices in the analysis to try to disentangle possible regional-scale differences in the effects of discharge on recruitment based on the available indices.

The downwelling index is described as the onshore/offshore component of Ekman transport, and is calculated based on geostrophic wind stress and the orientation of the adjacent coastline (PFEL, 2011). Index time series were obtained for 25 selected locations positioned along the shelf-break in the GOA at 1° longitudinal intervals (Fig. 5). Positive values denote upwelling-favorable winds and negative values denote downwelling-favorable winds. Downwelling-favorable winds at the shelf-break may not necessarily reflect local downwelling at the coast; however, measuring vertical transport near the coast was not the purpose of this index in our study. Rather, we used this index as an indicator of broad-scale, cross-shelf Ekman transport towards shore, which may be conducive to shoreward advection of slope-spawned larvae towards their nursery areas. The index captures links between variability in winds and subsequent ocean transport associated with large-scale climate processes related to variability in the NOI, NPGO, or PDO indices.

Analytical approach

Before our SEM analysis, we characterized spatial and/or seasonal variability in each environmental variable to select appropriate spatial and seasonal averages for the analysis. Freshwater discharge was available for two separate, relatively large regions and could not be analyzed at a smaller spatial scale. Climate indices (PDO, NOI, and NPGO) represent large-scale phenomena; hence only temporal variability was analyzed for these variables.

Because of large variability in downwelling-favorable winds along the GOA shelf break, we examined spatial patterns in upwelling using a hierarchical cluster analysis. Daily time series were compiled for each of the locations identified in Figure 5. Temporal patterns of variability

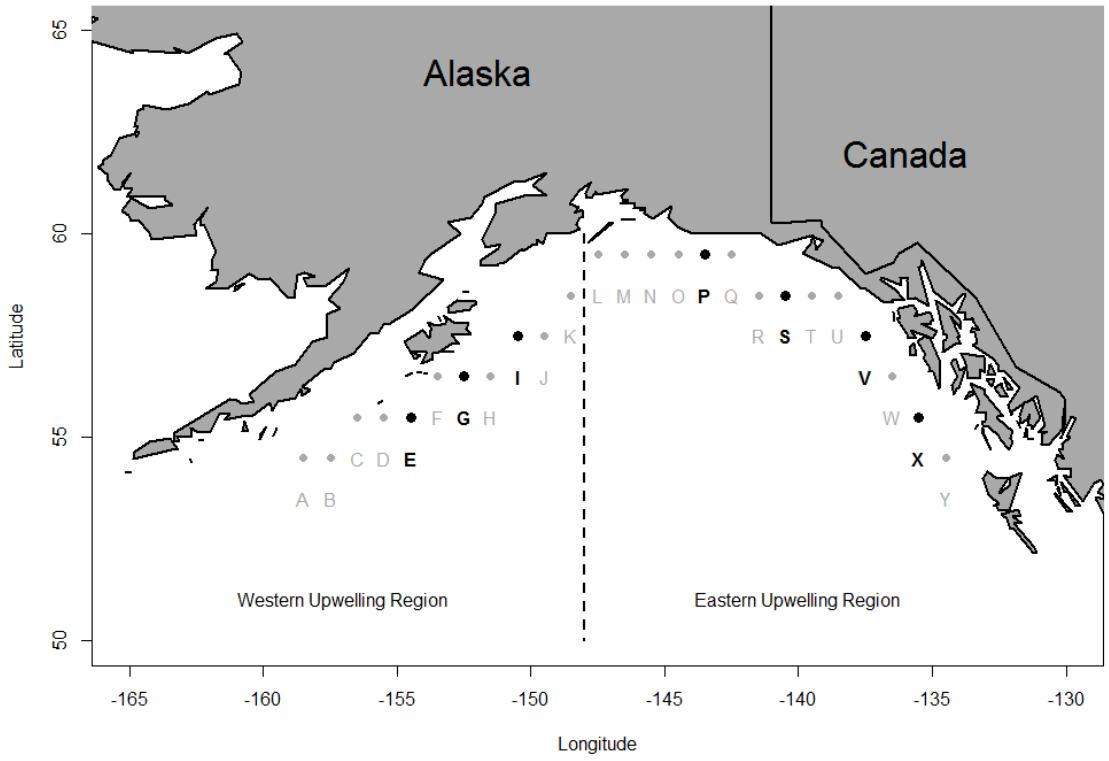

Figure 5. Downwelling index locations. Map showing downwelling index locations used in analysis. The dotted line marks the division between eastern and western downwelling regions. Black points (labeled in bold) denote locations used as subsamples to represent regional downwelling variability.

in these time series were compared among locations using pairwise Euclidean distances and Ward's minimum variance clustering (Ward, 1963). Results from this cluster analysis were mapped into dendograms, wherein locations whose time series showed similar patterns of variability were grouped together. These were used to visually identify groups of spatially continuous locations with similar patterns in variability in downwelling-favorable winds, each of which was considered a downwelling region. Within each identified region, representative locations were selected based on their proximity to the shelf break; upwelling indices at these locations were then averaged by region for further analyses.

A similar hierarchical cluster analysis was performed on the monthly time series of all environmental and climate indices in order to identify times of year showing coherent patterns of variability, thus defining seasonal patterns. For each variable, indices were averaged by month to form an interannual time series for each month. Temporal patterns of variability in these time series were compared among months using pairwise Euclidean distances and Ward's minimum variance clustering (Ward, 1963). The resulting dendograms were used to visually identify groups of months with similar interannual patterns of variability. Any consecutive months grouped together were considered a distinct "season" for the purposes of further analysis. Conversely, individual months showing no or limited similarity to the preceding or following months were considered their own distinct season. For regional indices, this analysis was performed separately for each region. In the event that a break was found between "December" and "January" for a given variable, cluster analysis was repeated using a non-calendar year (e.g., November of year *t* through October of year *t+1*) to investigate whether or not this was merely an artifact from using a calendar year. If so, the non-calendar year was used.

To examine relationships between recruitment and potential drivers we applied the SEM approach described in Bollen (1989) and Ullman et al. (2007), which can be briefly summarized as follows. First, a model outlining paths among climate variables, regional variables, and recruitment was specified. Next, each hypothesized path was translated into an equation from which parameters were estimated. These parameter estimates were used to construct a covariance matrix for the model, which was compared to the sample covariance matrix using a chi-square (χ^2) test. An insignificant χ^2 value reflects similar covariance matrices, indicating that the specified model is consistent with the observed data. Models with significant χ^2 values ($p < 0.05$) were therefore considered implausible and were ruled out as candidate models, while those with insignificant χ^2 values were considered plausible and examined further. Within a given model, each included path was tested for statistical significance separately.

While SEM allows for inclusion of latent variables, or variables for which no observed measurements are available (Bollen, 2002), such variables are seldom used in ecological analyses (Grace et al., 2010) and were not used here. Instead we used a variation of structural models more typically used by ecologists, in which latent variables are excluded:

$$\boldsymbol{y_t} = \boldsymbol{\Gamma x_t} + \boldsymbol{B y_t} + \boldsymbol{\zeta_t}, \qquad [2]$$

Where, if q is the number of endogenous variables and p is the number of exogenous variables, $\boldsymbol{y_t}$ denotes a q x 1 vector of endogenous and intermediary variables (e.g., recruitment and upwelling) at time t; $\boldsymbol{x_t}$ denotes a p x 1 vector of exogenous variables (e.g., PDO) at time t; $\boldsymbol{\Gamma}$ denotes a q x p matrix of regression coefficients between exogenous and endogenous variables; $\boldsymbol{B}$ denotes a q x q matrix of regression coefficients between endogenous and intermediary variables; and $\boldsymbol{\zeta_t}$ denotes a vector of error terms (Bollen, 1989). The placement of $\boldsymbol{y}$ on both sides of the equation is due to the ability of endogenous variables to predict one another in SEM when

they serve as intermediary variables (Bollen, 1989). Within each matrix of regression coefficients, the coefficients corresponding to a given pair of variables can be set to 0 if no relationship between those variables is hypothesized, set to a previously hypothesized fixed value, or estimated (Bollen, 1989; Ullman et al., 2007). Thus, relationships between endogenous variables and intermediary variables can be established in the $\boldsymbol{B}$ matrix by estimating the regression coefficient between them rather than fixing it at 0 (Bollen, 1989; Ullman et al., 2007). To visually represent the proposed relationships between variables, SEM models were mapped into path diagrams (e.g., Fig. 6).

We used two separate approaches of SEM analysis for each species. The first approach was a hypothesis-testing phase, in which we tested *a priori* hypotheses based on current information about each species' early life history. Each of these hypotheses was consistent with the overarching hypothesis that large-scale climate conditions affect the survival of young-of-year larvae, and their subsequent recruitment, through variability in cross-shelf advection towards suitable nursery grounds. For this phase, we applied a two-year lag between pre-selected seasonal indices of explanatory variables and age 2 recruitment in order to model variability in YCS against environmental conditions affecting early life stages during the hypothesized time periods at age 0. Because we found little support for these *a priori* hypotheses, we extended the analyses to include an exploratory phase, in which we examined potential effects of selected large-scale and regional variables at other biologically reasonable lags. For this phase, we applied lags ranging from zero to two years between explanatory variables and age 2 recruitment in order to model variability in YCS against environmental conditions affecting larvae and juveniles between hatching and settlement at age 2.

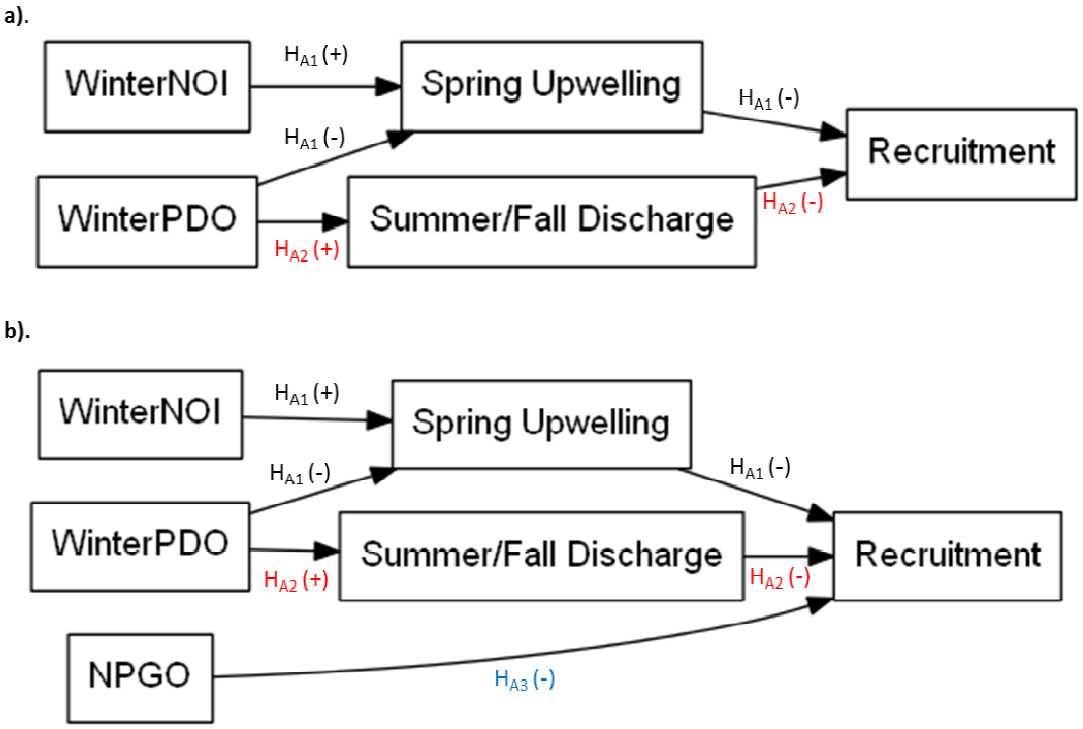

Figure 6. Hypothesized path diagrams. Path diagrams showing hypothesized relationships between variables. Relationships are shown for (a) sablefish and (b) POP. Arrows point from exogenous variables to endogenous variables. Edge labels denote the overarching hypothesis that a given path is part of as well as the hypothesized sign of that path.

To form *a priori* hypotheses about the relationship between environmental variables and recruitment processes, it is important to select appropriate spatial and temporal periods over which the hypothesized mechanisms operate (e.g., Mueter et al., 2005). Sablefish larvae are present on the shelf during April and May (Miriam Doyle, University of Washington, Seattle, pers. comm.), which coincides with the timing of larval parturition for POP (Gunderson, 1971, 1972, 1977). It is likely during this time period that downwelling-favorable winds at the shelf break play a role in enhancing onshore advection for both species. Because the ACC is located close to shore (Royer, 1982; Stabeno et al., 2004), freshwater discharge may play a role in the advection of sablefish larvae during late summer and fall (approximately July through September), just prior to their nearshore settlement (Rutecki and Varosi, 1997a, b). While the timing for POP settlement is unknown, their larvae may reach the ACC during the same approximate time period as sablefish larvae if sablefish hatching and POP parturition occur along the slope during the same approximate time period. Therefore, during the hypothesis-testing phase of our analysis, we used downwelling during April and May and discharge during summer (July – September) and fall (October – November) as the hypothesized time periods during which these variables are related to recruitment of each species. For the PDO and the NOI, we used winter indices because large-scale wintertime conditions tend to relate to groundfish recruitment more strongly (Hollowed and Wooster, 1992), likely through delayed effects on spring and summer regional variables, consistent with their use in other studies. We used an annual NPGO index because our cluster analysis did not suggest distinct seasonal patterns of variability.

Based on these considerations, we specifically tested the following *a priori* hypotheses during our hypothesis-testing phase:

H_{A1}: Recruitment is negatively related to upwelling-favorable winds in the E GOA during mid-spring, which in turn are positively related to winter NOI and negatively related to winter PDO.

H_{A2}: Recruitment is negatively related to total freshwater discharge during summer or fall, which in turn is positively related to winter PDO.

H_{A3}: Recruitment shows a negative relationship to the NPGO.

H_{A1} and H_{A2} apply to each species, but H_{A3} was only hypothesized for POP. To test these hypotheses, a series of alternative SEM models were compared for each species, including:

1) A full model containing all variables at appropriate lags that tested all applicable hypotheses simultaneously (Fig. 6),

2) Multiple reduced models testing all possible combinations of hypotheses at a time (e.g., H_{A1} and H_{A2}; H_{A1} only, H_{A2} only, etc.), and

3) Variants of each model wherein the hypothesized seasonal time period for each variable was represented by alternate seasonal averages, if applicable. For example, mid-spring downwelling was represented by April downwelling in one model and May downwelling in another.

Because H_{A1} and H_{A2} each involve multiple sequential relationships, these hypotheses were rejected unless all such relationships were found to be significant (at $\alpha = 0.05$) within one or more plausible candidate structural models. For instance, if a plausible model contained a significant path between summer discharge and recruitment and an insignificant path between winter PDO and summer discharge, this model would be insufficient for rejecting the null hypothesis in favor of H_{A2}. Therefore, for each of the alternative hypotheses, the null hypothesis (H_0) is that one or more of the proposed relationships between variables is insignificant.

In the exploratory analyses, recruitment was modeled against an extended range of seasonal lags for each variable throughout each species' early life history (age 0 through age 2), testing different combinations of climate and regional explanatory variables. Although exploratory, these models still contained assumptions of sequential causation between climate and regional variables; therefore, climate variables at each seasonal lag were always modeled with regional variables at concurrent or later seasonal lags. We also considered models that contained only climate indices with no intermediary variables in order to test for direct links between climate variables and recruitment that may not be evident in regional indices.

The large number of models tested in the exploratory phase contains an increased risk of Type I error. We address this by employing multiple criteria by which models were eliminated from the analysis. Implausible exploratory models (i.e., those with significant χ^2 values) were excluded, and remaining candidate models were compared using the small-sample Akaike Information Criterion (AICc); if the difference in AICc values (ΔAICc) was larger than 2, the model with the smallest AICc was chosen as the final model (Burnham and Anderson, 2002). If multiple alternative models had similar support (ΔAICc < 2), the most parsimonious model was chosen. In the event that models with similar support also had the same number of parameters, all such models were equally considered. Consequently, all models with ΔAICc values > 2 relative to the smallest AICc value were eliminated from the analysis alongside models deemed implausible according to their χ^2 values, reducing the potential for spurious relationships. Additionally, we took into account incidents in which multiple final candidate models contained the same significant relationship, strengthening the evidence for an effect. The Adjusted Goodness of Fit Index (AGFI) was also reported to provide information on each model's fit to the data, but was not used to inform model selection. The AGFI values range from 0 (no fit) to 1

(perfect fit). The exploratory phase was performed in such a way that relationships during each year of each species' early life history were examined separately; i.e., models testing relationships during age 0 were only compared with other models testing relationships during age 0, and likewise for ages 1 and 2.

The statistical software package R, version 2.14.0 (R Development Core Team, 2011), was used for all analyses. Structural models were fit using the 'sem' package (Fox, 2006).

Results

Cluster analysis

Two distinct downwelling regions within the GOA were identified via cluster analysis: one for the E GOA and one for the W GOA, with a break point between locations K (147.5° west) and L (148.5° west; Fig. 5). The location of this break point may be a function of the abrupt change in coastline orientation that occurs here, with the E GOA coastline oriented northwest-southeast and the W GOA coastline oriented southwest-northeast. The downwelling index in the E GOA indicated a stronger seasonal signal, with stronger downwelling-favorable conditions during fall and winter; in contrast, the W GOA exhibited a weaker seasonal pattern, weaker wintertime downwelling-favorable winds, and a longer period of upwelling-favorable winds (Fig. 7). The most striking difference occurred during the latter half of the year (approximately mid-July through December), when the E GOA region was dominated by downwelling winds, whereas winds in the W GOA region were primarily upwelling-favorable with occasional reversals.

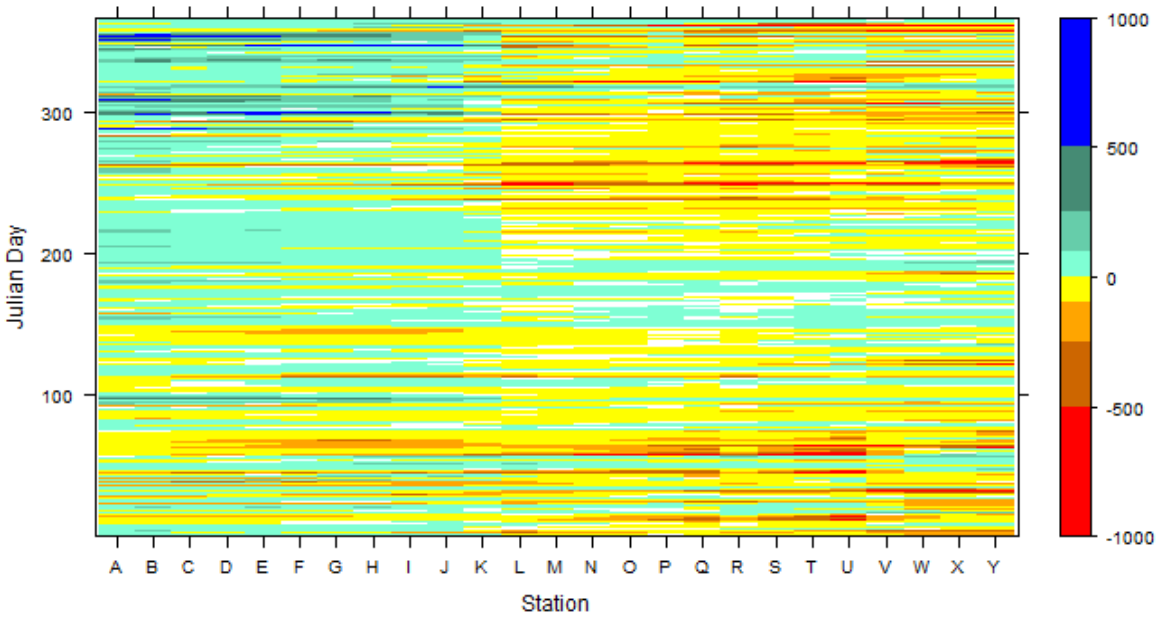

Figure 7. Downwelling by location and Julian day. Hovmöller diagram showing downwelling index values by Julian day and longitude. Daily values are averaged across years 1967 – 2011 and longitude is divided between locations A – Y from west to east (see Fig. 5). Warm colors (negative values) represent downwelling-favorable winds and cool colors (positive values) represent upwelling-favorable winds.

For the locations representing the E GOA nine distinct monthly groupings ("seasons") with respect to downwelling were identified (Fig. 8) because several months did not cluster with any other group. Because the "winter" season included November of year *t* through January of year *t+1*, the time series' first year (1967) had to be excluded from the sablefish analysis and only years 1968 – 2009 were used. For the locations representing the W GOA, eight distinct seasons were identified (Fig. 9). For E GOA discharge, four distinct seasons were selected: early winter (Nov – Jan), late winter (Feb – Mar), April, and summer/fall (May – Oct). For C GOA discharge, three seasons were selected: winter (Nov – Feb), early spring (Mar – Apr), and summer/fall (May – Oct). For total discharge, five seasons were selected: winter (Dec – Jan), early spring (Feb – Apr), late spring (May – Jun), summer (Jul – Sep), and fall (Oct – Nov).

Seasons selected for the NOI included winter (Sep – Apr) and summer (May – Aug). For the PDO, three seasons were selected: winter (Jan – Mar), spring/summer (Apr – Sep), and late fall (Oct – Dec). The NPGO showed no obvious seasonal patterns; therefore, an annual mean NPGO index was used in all further analyses.

SEM analysis

Sablefish

In the hypothesis-testing phase for sablefish, both *a priori* hypotheses (H_{A1} and H_{A2}) were rejected. As previously mentioned, H_{A3} was not proposed and therefore was not tested for sablefish. A total of 12 models were tested in the hypothesis-testing SEM phase; of these, 11 models had the insignificant χ^2 values required to be considered as candidate models. Candidate models testing both H_{A1} and H_{A2} simultaneously had less support than smaller models testing

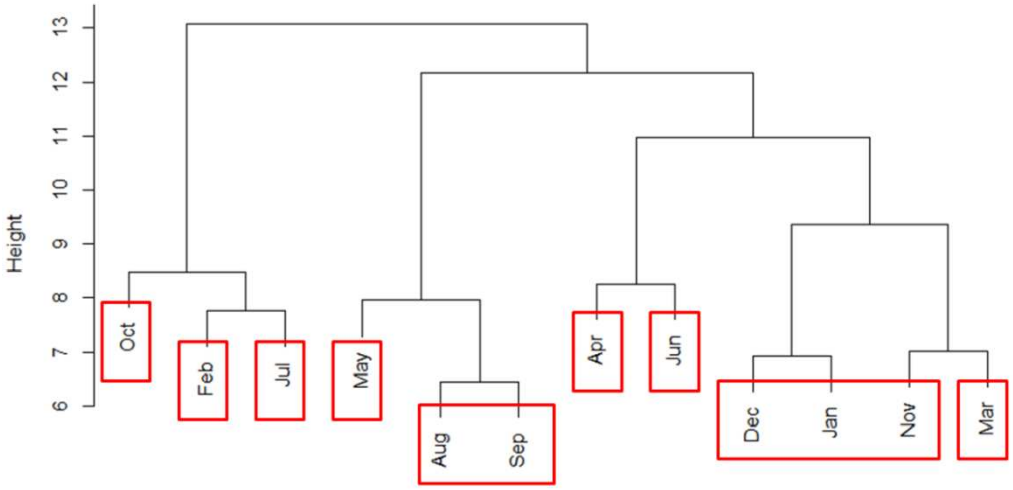

Figure 8. Eastern GOA downwelling dendogram. Ward's minimum variance dendogram resulting from cluster analysis of the monthly eastern GOA downwelling index. Boxes mark groups selected as distinct seasonal lags.

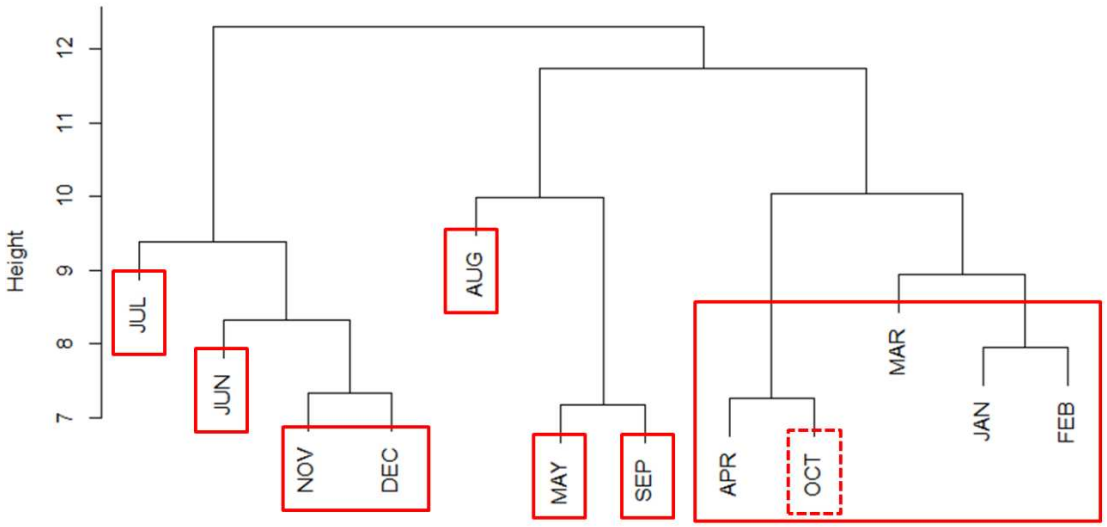

Figure 9. Western GOA downwelling dendogram. Ward's minimum variance dendogram resulting from cluster analysis of the monthly western GOA downwelling index. Boxes mark groups selected as distinct seasonal lags. The dotted box around October indicates its exclusion from the larger cluster containing it, due to its being nonconsecutive with those months.

one of these hypotheses at a time (Table 2). The two best candidate models both tested H_{A2} only, but contained no paths that were individually significant. Among the remaining models, the most consistently significant paths were a negative correlation between winter PDO and winter NOI and a negative relationship between winter NOI and March (E GOA) upwelling-favorable winds. No models contained any significant paths between environmental variables and recruitment and the coefficients of variation for recruitment (endogenous R^2 in Table 2) were generally smaller than 5%.

The exploratory analysis indicated that sablefish recruitment was negatively related to above average late winter and early spring discharge at both age 1 and age 2, and positively related to stronger July upwelling-favorable winds at age 1 (Fig. 10). Recruitment was unrelated to downwelling or discharge conditions during the larval and early juvenile phase (age 0). A total of 37 models were tested examining relationships during age 0; of these, 28 models had insignificant χ^2 values and the 10 best models had similar AICc values and the same number of parameters (Table 3). Only three significant paths were found within these models: a positive relationship between winter PDO and early spring (total) discharge, a negative relationship between winter PDO and summer/fall (E GOA) discharge, and a negative correlation between winter PDO and winter NOI. Coefficients of variation for recruitment were all below 5% in these models.

Recruitment was positively related to July upwelling-favorable winds and negatively related to late winter discharge in the E GOA during age 1. Of the 44 models testing relationships during age 1, 36 models had insignificant χ^2 values; the 15 best models had similar AICc values and the same number of parameters (Table 4). Of these, 4 models showed a significant positive relationship between July (E GOA) upwelling-favorable winds and

Table 2 Sablefish analysis results (hypothesis-testing phase): Summary statistics for SEM models from the sablefish hypothesis-testing phase. Summary statistics for individual paths are only included for plausible models. Arrows point from exogenous to endogenous variables; double-headed arrows denote correlations with no causal relationship hypothesized. ΔAICc is given relative to the model with the lowest AICc; K represents the number of parameters. Shaded cells indicate p-values ≤ 0.05.

Hypotheses Tested	Adjusted Goodness-of-fit	Pr (>|χ^2|)	ΔAICc	K	Path	Path p-value	Path β-estimate	Endogenous Variable R^2	H_0 Outcome
H_{A1}, H_{A2}	0.76	0.10	14.80	11	April (E GOA) Upwelling → Recruitment	0.31	-0.16	0.04	Failure to Reject
					Summer (Total) Discharge → Recruitment	0.38	-0.14		
					Winter NOI → April (E GOA) Upwelling	0.86	0.03	0.02	
					Winter PDO → April (E GOA) Upwelling	0.56	-0.11		
					Winter PDO → Summer (Total) Discharge	0.06	-0.28	0.08	
					Winter PDO ←→ Winter NOI	< 0.01	-0.57	NA	
H_{A1}, H_{A2}	0.52	< 0.01	29.20	10					Failure to Reject

Table 2 (continued)

Hypotheses Tested	Adjusted Goodness-of-fit	Pr (>|χ^2|)	ΔAICc	K	Path	Path p-value	Path β-estimate	Endogenous Variable R^2	H_0 Outcome
H_{A1}, H_{A2}	0.83	0.27	12.27	11	March (E GOA) Upwelling → Recruitment	0.55	-0.09	0.02	Failure to Reject
					Summer (Total) Discharge → Recruitment	0.40	-0.13		
					Winter NOI → March (E GOA) Upwelling	0.02	-0.43	0.15	
					Winter PDO → March (E GOA) Upwelling	0.68	-0.07		
					Winter PDO → Summer (Total) Discharge	0.06	-0.28	0.08	
					Winter PDO ←→ Winter NOI	< 0.01	-0.57	NA	
H_{A1}, H_{A2}	0.80	0.20	13.13	11	May (E GOA) Upwelling → Recruitment	0.74	0.05	0.01	Failure to Reject
					Summer (Total) Discharge → Recruitment	0.52	-0.10		
					Winter NOI → May (E GOA) Upwelling	0.06	-0.34	0.08	
					Winter PDO → May (E GOA) Upwelling	0.32	-0.18		
					Winter PDO → Summer (Total) Discharge	0.06	-0.28	0.08	
					Winter PDO ←→ Winter NOI	< 0.01	-0.57	NA	

Table 2 (continued)

Hypotheses Tested	Adjusted Goodness-of-fit	Pr (>|χ^2|)	ΔAICc	K	Path	Path p-value	Path β-estimate	Endogenous Variable R^2	H_0 Outcome
H_{A1}, H_{A2}	0.90	0.57	10.04	11	March (E GOA) Upwelling → Recruitment	0.71	-0.06	< 0.01	Failure to Reject
					Fall (Total) Discharge → Recruitment	0.87	0.02		
					Winter NOI → March (E GOA) Upwelling	0.02	-0.43	0.15	
					Winter PDO → March (E GOA) Upwelling	0.68	-0.07		
					Winter PDO → Fall (Total) Discharge	0.18	-0.21	0.04	
					Winter PDO ←→ Winter NOI	< 0.01	-0.57	NA	
H_{A1}, H_{A2}	0.85	0.33	11.71	11	April (E GOA) Upwelling → Recruitment	0.39	-0.13	0.02	Failure to Reject
					Fall (Total) Discharge → Recruitment	0.93	0.01		
					Winter NOI → April (E GOA) Upwelling	0.86	0.03	0.02	
					Winter PDO → April (E GOA) Upwelling	0.56	-0.11		
					Winter PDO → Fall (Total) Discharge	0.18	-0.21	0.04	
					Winter PDO ←→ Winter NOI	< 0.01	-0.57	NA	

Table 2 (continued)

Hypotheses Tested	Adjusted Goodness-of-fit	Pr (>|χ^2|)	ΔAICc	K	Path	Path p-value	Path β-estimate	Endogenous Variable R^2	H_0 Outcome
H_{A1}, H_{A2}	0.86	0.41	11.10	11	May (E GOA) Upwelling → Recruitment	0.61	0.08	0.01	Failure to Reject
					Fall (Total) Discharge → Recruitment	0.74	0.05		
					Winter NOI → May (E GOA) Upwelling	0.06	-0.34	0.08	
					Winter PDO → May (E GOA) Upwelling	0.32	-0.18		
					Winter PDO → Fall (E GOA) Upwelling	0.18	-0.21	0.04	
					Winter PDO ←→ Winter NOI	< 0.01	-0.57	NA	
H_{A1}	0.92	0.50	4.07	8	March (E GOA) Upwelling → Recruitment	0.69	-0.06	< 0.01	Failure to Reject
					Winter NOI → March (E GOA) Upwelling	0.02	-0.43	0.15	
					Winter PDO → March (E GOA) Upwelling	0.68	-0.07		
					Winter PDO ←→ Winter NOI	< 0.01	-0.57	NA	
H_{A1}	0.90	0.43	4.37	8	April (E GOA) Upwelling → Recruitment	0.39	-0.13	0.02	Failure to Reject
					Winter NOI → April (E GOA) Upwelling	0.86	0.03	0.02	
					Winter PDO → April (E GOA) Upwelling	0.56	-0.11		
					Winter PDO ←→ Winter NOI	< 0.01	-0.57	NA	

Table 2 (continued)

Hypotheses Tested	Adjusted Goodness-of-fit	Pr (>|χ^2|)	ΔAICc	K	Path	Path p-value	Path β-estimate	Endogenous Variable R^2	H_0 Outcome
H_{A1}	0.88	0.36	4.74	8	May (E GOA) Upwelling → Recruitment	0.65	0.07	< 0.01	Failure to Reject
					Winter NOI → May (E GOA) Upwelling	0.06	-0.34	0.08	
					Winter PDO → May (E GOA) Upwelling	0.32	-0.18		
					Winter PDO ←→ Winter NOI	< 0.01	-0.57	NA	
H_{A2}	1.00	0.91	0.00	5	Fall (Total) Discharge → Recruitment	0.82	0.04	< 0.01	Failure to Reject
					Winter PDO → Fall (Total) Discharge	0.18	-0.21	0.04	
H_{A2}	0.99	0.71	0.12	5	Summer (Total) Discharge → Recruitment	0.48	-0.11	0.01	Failure to Reject
					Winter PDO → Summer (Total) Discharge	0.06	-0.28	0.08	

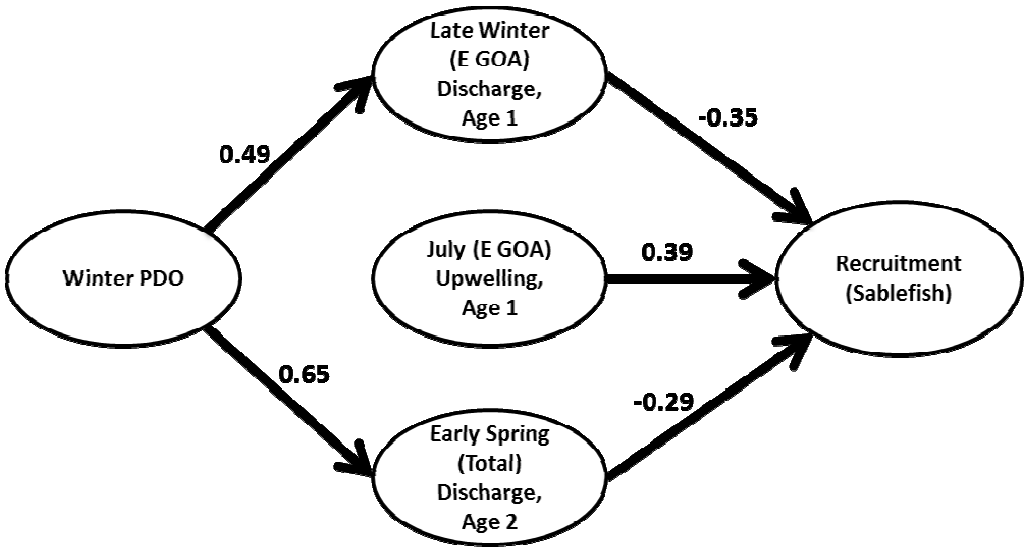

Figure 10. Sablefish relationships. Diagram mapping significant relationships found in exploratory sablefish SEM analysis. Only relationships between environmental variables and recruitment are represented, including sequential relationships. Arrows point from exogenous to endogenous variables. Numbers denote parameter estimates.

Table 3 Sablefish analysis results (exploratory phase, age 0): Summary statistics from exploratory sablefish analysis examining conditions during age 0. Data are provide for the best SEM candidate models, sorted by ΔAICc relative to the model with the lowest AICc. Arrows point from exogenous to endogenous variables; double-headed arrows denote correlations with no causal relationship hypothesized. K represents the number of parameters. Shaded cells indicate p-values ≤ 0.05.

Adjusted Goodness-of-fit	Pr (>|χ^2|)	ΔAICc	K	Path	Path p-value	Path β-estimate	Endogenous Variable R^2
1.00	0.99	0.00	5	Summer/Fall (E GOA) Discharge → Recruitment	0.67	0.07	< 0.01
				Winter PDO → Summer/Fall (E GOA) Discharge	0.02	-0.33	0.11
1.00	0.93	0.01	5	June (E GOA) Upwelling → Recruitment	0.80	0.04	< 0.01
				Winter PDO → June (E GOA) Upwelling	0.05	-0.29	0.08
1.00	0.88	0.02	5	July (E GOA) Upwelling → Recruitment	0.89	0.02	< 0.01
				Winter PDO → July (E GOA) Upwelling	0.65	-0.07	< 0.01
1.00	0.87	0.03	5	May (E GOA) Upwelling → Recruitment	0.65	0.07	< 0.01
				Winter PDO → May (E GOA) Upwelling	0.94	0.01	< 0.01
0.99	0.79	0.07	5	April (E GOA) Upwelling → Recruitment	0.39	-0.13	0.02
				Winter PDO → April (E GOA) Upwelling	0.41	-0.13	0.02
0.96	0.54	0.38	5	Early Spring (Total) Discharge → Recruitment	0.63	0.07	0.01
				Winter PDO → Early Spring (Total) Discharge	< 0.01	0.65	0.43
0.90	0.30	1.08	5	April (E GOA) Upwelling → Recruitment	0.39	-0.13	0.02
				NPGO → April (E GOA) Upwelling	0.56	0.09	0.01
0.89	0.27	1.20	5	July (E GOA) Upwelling → Recruitment	0.89	0.02	< 0.01
				Winter NOI → July (E GOA) Upwelling	0.71	0.06	< 0.01
0.86	0.23	1.44	5	April (E GOA) Upwelling → Recruitment	0.39	-0.13	0.02
				Winter NOI → April (E GOA) Upwelling	0.54	0.10	0.01
0.86	0.22	1.52	5	Early Spring (Total) Discharge → Recruitment	0.88	-0.02	< 0.01
				Winter PDO ←→ Winter NOI	< 0.01	-0.57	NA

Table 4 Sablefish analysis results (exploratory phase, age 1): Summary statistics from exploratory sablefish analysis examining conditions during age 1. Data are provided for the best SEM candidate models, sorted by ΔAICc relative to the model with the lowest AICc. Arrows point from exogenous to endogenous variables; double-headed arrows denote correlations with no causal relationship hypothesized. K represents the number of parameters. Shaded cells indicate p-values ≤ 0.05.

Adjusted Goodness-of-fit	Pr (>|χ^2|)	ΔAICc	k	Path	Path p-value	Path β-estimate	Endogenous Variable R^2
1.00	0.97	0.00	5	May (E GOA) Upwelling → Recruitment	0.56	-0.09	0.01
				Winter PDO → May (E GOA) Upwelling	0.89	0.02	< 0.01
1.00	0.90	0.01	5	April (E GOA) Upwelling → Recruitment	0.18	0.20	0.04
				Winter PDO → April (E GOA) Upwelling	0.38	-0.13	0.02
1.00	0.89	0.02	5	July (E GOA) Upwelling → Recruitment	0.01	0.37	0.14
				Winter PDO → July (E GOA) Upwelling	0.63	-0.07	0.01
1.00	0.87	0.02	5	June (E GOA) Upwelling → Recruitment	0.50	0.10	0.01
				Winter PDO → June (E GOA) Upwelling	0.04	-0.30	0.09
1.00	0.82	0.05	5	July (E GOA) Upwelling → Recruitment	0.01	0.37	0.14
				NPGO → July (E GOA) Upwelling	0.69	-0.06	< 0.01
0.98	0.64	0.21	5	March (E GOA) Upwelling → Recruitment	0.07	-0.27	0.07
				NPGO → March (E GOA) Upwelling	0.06	-0.28	0.08
0.98	0.64	0.22	5	Summer (Total) Discharge → Recruitment	0.16	-0.21	0.05
				Winter PDO → Summer (Total) Discharge	0.05	-0.28	0.08
0.98	0.63	0.23	5	Summer/Fall (E GOA) Discharge → Recruitment	0.24	-0.18	0.03
				Winter PDO → Summer/Fall (E GOA) Discharge	0.02	-0.34	0.11
0.91	0.31	1.01	5	Early Spring (Total) Discharge → Recruitment	0.22	-0.19	0.04
				Winter PDO → Early Spring (Total) Discharge	< 0.01	0.65	0.43

Table 4 (continued)

Adjusted Goodness-of-fit	Pr (>|χ^2|)	ΔAICc	k	Path	Path p-value	Path β-estimate	Endogenous Variable R^2
0.87	0.23	1.41	5	July (E GOA) Upwelling → Recruitment	0.01	0.37	0.14
				Spring/Summer PDO → July (E GOA) Upwelling	0.95	-0.01	< 0.01
0.86	0.22	1.50	5	Summer (Total) Discharge → Recruitment	0.16	-0.21	0.05
				Spring/Summer PDO → Summer (Total) Discharge	0.75	-0.05	< 0.01
0.85	0.20	1.62	5	Late Winter (E GOA) Discharge → Recruitment	0.02	-0.34	0.12
				Winter PDO → Late Winter (E GOA) Discharge	< 0.01	0.49	0.24
0.85	0.20	1.64	5	April (E GOA) Upwelling → Recruitment	0.18	0.20	0.04
				Winter NOI → April (E GOA) Upwelling	0.50	0.10	0.01
0.83	0.17	1.88	5	July (E GOA) Upwelling → Recruitment	0.01	0.37	0.14
				Winter NOI → July (E GOA) Upwelling	0.68	0.06	< 0.01
0.82	0.16	1.95	5	Winter PDO → Recruitment	0.96	-0.01	< 0.01
				Winter PDO ←→ Winter NOI	< 0.01	-0.57	NA

recruitment. One model showed a sequential set of significant relationships wherein winter PDO was positively related to late winter (E GOA) discharge, which was negatively related to recruitment. Six models showed no significant relationships.

Sablefish recruitment showed a negative relationship to total discharge during early spring of age 2. A total of 43 models were tested to examine relationships during age 2, 37 of which had insignificant χ^2 values. The 11 best models had similar AICc values and the same number of parameters (Table 5). One model showed a sequential set of significant relationships wherein winter PDO was positively related to early spring (total) discharge, which was negatively related to recruitment. Other models showed significant relationships between winter PDO and E GOA discharge during late winter and summer/fall, and 6 models showed no significant relationships.

POP

In the hypothesis-testing phase for POP, all three *a priori* hypotheses were rejected; however, in the exploratory analysis, recruitment was found to be negatively related to June upwelling-favorable winds in both the E and W GOA during ages 0 and 1, and positively related to late spring total discharge during age 1 (Fig. 11).

Though we found little support for our *a priori* hypotheses for POP during the hypothesis-testing SEM phase, there was support for some components of H_{A1}; specifically, we found that recruitment of POP was positively related to stronger downwelling-favorable winds during late spring. Of the 35 models tested during this phase, 13 models had insignificant χ^2 values and were thus considered as candidate models. Three models contained a significant negative relationship between June (E GOA) upwelling-favorable winds and recruitment, and 2

Table 5 Sablefish analysis results (exploratory phase, age 2): Summary statistics from exploratory sablefish analysis examining conditions during age 2. Data are provided for the best SEM candidate models, sorted by ΔAICc relative to the model with the lowest AICc. Arrows point from exogenous to endogenous variables; double-headed arrows denote correlations with no causal relationship hypothesized. K represents the number of parameters. Shaded cells indicate p-values ≤ 0.05.

Adjusted Goodness-of-fit	Pr (>|χ^2|)	ΔAICc	K	Path	Path p-value	Path β-estimate	Endogenous Variable R^2
1.00	1.00	0.00	5	July (E GOA) Upwelling → Recruitment	0.44	-0.12	0.01
				NPGO → July (E GOA) Upwelling	0.69	-0.06	< 0.01
1.00	0.96	< 0.01	5	March (E GOA) Upwelling → Recruitment	0.99	-0.01	< 0.01
				NPGO → March (E GOA) Upwelling	0.06	-0.28	0.08
1.00	0.83	0.04	5	Winter PDO → Recruitment	0.09	-0.25	0.06
				Winter PDO ←→ Winter NOI	< 0.01	-0.57	NA
0.99	0.79	0.07	5	Summer (Total) Discharge → Recruitment	0.41	0.13	0.02
				Spring/Summer PDO → Summer (Total) Discharge	0.75	-0.05	< 0.01
0.99	0.75	0.10	5	July (E GOA) Upwelling → Recruitment	0.44	-0.12	0.01
				Spring/Summer PDO → July (E GOA) Upwelling	0.95	-0.01	< 0.01
0.97	0.57	0.33	5	Early Spring (Total) Discharge → Recruitment	0.05	-0.29	0.09
				Winter PDO → Early Spring (Total) Discharge	< 0.01	0.65	0.43
0.94	0.43	0.62	5	April (E GOA) Upwelling → Recruitment	0.97	-0.01	< 0.01
				Winter NOI → April (E GOA) Upwelling	0.50	0.10	0.01
0.94	0.41	0.69	5	March (E GOA) Upwelling → Recruitment	0.99	< 0.01	< 0.01
				Winter NOI → March (E GOA) Upwelling	0.01	-0.35	0.12
0.93	0.40	0.70	5	July (E GOA) Upwelling → Recruitment	0.44	-0.12	0.01
				Winter NOI → July (E GOA) Upwelling	0.68	0.06	< 0.01

Table 5 (continued)

Adjusted Goodness-of-fit	Pr (>|χ^2|)	ΔAICc	K	Path	Path p-value	Path β-estimate	Endogenous Variable R^2
0.85	0.20	1.63	5	Late Winter (E GOA) Discharge → Recruitment	0.25	-0.18	0.03
				Winter PDO → Late Winter (E GOA) Discharge	< 0.01	0.49	0.24
0.85	0.20	1.66	5	Summer/Fall (E GOA) Discharge → Recruitment	0.15	0.22	0.05
				Winter PDO → Summer/Fall (E GOA) Discharge	0.02	-0.34	0.11

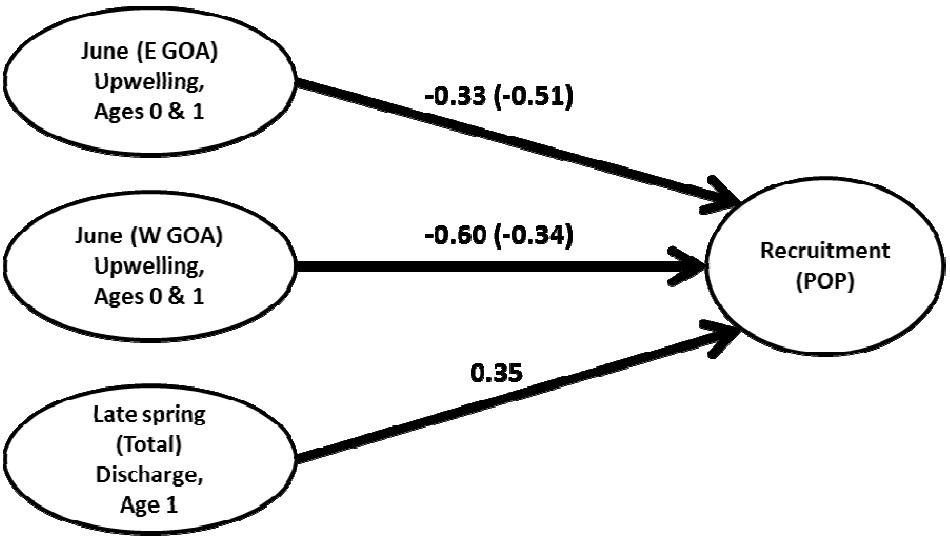

Figure 11. Pacific ocean perch relationships. Diagram mapping significant relationships found in exploratory POP SEM analysis. Only relationships between environmental variables and recruitment are represented. Arrows point from exogenous to endogenous variables. Numbers denote parameter estimates for relationships during age 0 and age 1 (in parentheses).

models contained a significant negative relationship between June (W GOA) upwelling-favorable winds and recruitment. A significant negative correlation between winter PDO and winter NOI was shown in 11 plausible models (Table 6). The best candidate model tested H_{A3} only and contained no significant paths.

The exploratory SEM phase indicated several significant relationships between POP recruitment and environmental variables at multiple lags. Recruitment of POP was negatively related to stronger June upwelling-favorable winds in the western GOA during age 0. A total of 49 models were tested examining relationships during age 0, 35 of which had insignificant χ^2 values. Of these, the 9 best models had similar AICc values and the same number of parameters (Table 7). Two of these models showed a significant negative relationship between June (W GOA) upwelling-favorable winds and recruitment. March (E GOA) upwelling-favorable winds showed a negative relationship to the NPGO in one model and to winter NOI in another. In 5 models, no significant relationships were found.

POP were also found to be negatively associated with stronger June upwelling-favorable winds in both the eastern and western GOA during age 1, as well as with total discharge during late spring. A total of 51 models were tested examining relationships during age 1, 42 of which had insignificant χ^2 values. The 9 best models had similar AICc values and the same number of parameters (Table 8). Three of these models showed a significant negative relationship between June (E GOA) upwelling-favorable winds and recruitment, and 3 others showed a significant negative relationship between June (W GOA) upwelling-favorable winds and recruitment. March (E GOA) upwelling-favorable winds showed negative relationships to both the NPGO and winter NOI, respectively, and late spring (total) discharge showed a significant positive relationship to recruitment in one model.

Table 6 Pacific ocean perch analysis results (hypothesis-testing phase): Summary statistics for SEM models from the POP hypothesis-testing phase. Summary statistics for individual paths are only included for plausible models. Arrows point from exogenous to endogenous variables; double-headed arrows denote correlations with no causal relationship hypothesized. ΔAICc is given relative to the model with the lowest AICc; K represents the number of parameters. Shaded cells indicate p-values ≤ 0.05.

Hypotheses Tested	Adjusted Goodness-of-fit	Pr (>|χ^2|)	ΔAICc	K	Path	Path p-value	Path β-estimate	Endogenous Variable R^2	H_0 Outcome
All	0.58	< 0.01	39.47	13					Failure to Reject
All	0.56	< 0.01	40.92	13					Failure to Reject
All	0.60	< 0.01	40.11	13					Failure to Reject
All	0.59	0.01	38.62	13					Failure to Reject
All	0.58	< 0.01	41.09	13					Failure to Reject
All	0.71	0.10	30.72	13	April (E GOA) Upwelling → Recruitment	0.52	-0.11	0.02	Failure to Reject
					Fall (Total) Discharge → Recruitment	0.65	-0.08		
					NPGO → Recruitment	0.83	0.04		
					Winter NOI → April (E GOA) Upwelling	0.76	0.06	0.01	
					Winter PDO → April (E GOA) Upwelling	0.87	-0.03		
					Winter PDO → Fall (Total) Discharge	0.07	-0.30	0.09	
					Winter PDO ←→ Winter NOI	0.01	-0.54	NA	

Table 6 (continued)

Hypotheses Tested	Adjusted Goodness-of-fit	Pr (>|χ^2|)	ΔAICc	K	Path	Path p-value	Path β-estimate	Endogenous Variable R^2	H_0 Outcome
All	0.67	0.05	32.96	13					Failure to Reject
All	0.74	0.17	29.10	13	June (E GOA) Upwelling → Recruitment	0.04	-0.33	0.12	Failure to Reject
					Fall (Total) Discharge → Recruitment	0.56	-0.09		
					NPGO → Recruitment	0.86	-0.03		
					Winter NOI → June (E GOA) Upwelling	0.14	-0.29	0.11	
					Winter PDO → June (E GOA) Upwelling	0.06	-0.37		
					Winter PDO → Fall (Total) Discharge	0.07	-0.30	0.09	
					Winter PDO ←→ Winter NOI	0.01	-0.54	NA	
All	0.72	0.11	30.39	13	Winter/Spring (W GOA) Upwelling → Recruitment	0.27	-0.19	0.05	Failure to Reject
					Fall (Total) Discharge → Recruitment	0.87	-0.03		
					NPGO → Recruitment	0.62	0.09		
					Winter NOI → Winter/Spring (W GOA) Upwelling	0.03	0.38	0.28	
					Winter PDO → Winter/Spring (W GOA) Upwelling	0.23	-0.21		
					Winter PDO → Fall (Total) Discharge	0.07	-0.30	0.09	
					Winter PDO ←→ Winter NOI	0.01	-0.54	NA	

Table 6 (continued)

Hypotheses Tested	Adjusted Goodness-of-fit	Pr (>|χ^2|)	ΔAICc	K	Path	Path p-value	Path β-estimate	Endogenous Variable R^2	H_0 Outcome
All	0.71	0.09	31.03	13	June (W GOA) Upwelling → Recruitment	< 0.01	-0.64	0.42	Failure to Reject
					Fall (Total) Discharge → Recruitment	0.52	-0.09		
					NPGO → Recruitment	0.31	-0.14		
					Winter NOI → June (W GOA) Upwelling	0.25	-0.23	0.05	
					Winter PDO → June (W GOA) Upwelling	0.28	-0.22		
					Winter PDO → Fall (Total) Discharge	0.07	-0.30	0.09	
					Winter PDO ←→ Winter NOI	0.01	-0.54	NA	
H_{A1}, H_{A3}	0.64	0.03	21.17	10					Failure to Reject
H_{A1}, H_{A3}	0.60	0.02	22.69	10					Failure to Reject
H_{A1}, H_{A3}	0.68	0.06	19.57	10	June (E GOA) Upwelling → Recruitment	0.05	-0.32	0.11	Failure to Reject
					NPGO → Recruitment	0.85	-0.03		
					Winter NOI → June (E GOA) Upwelling	0.14	-0.29	0.11	
					Winter PDO → June (E GOA) Upwelling	0.06	-0.37		
					Winter PDO ←→ Winter NOI	0.01	-0.55	NA	
H_{A1}, H_{A3}	0.64	0.03	21.42	10					Failure to Reject

Table 6 (continued)

Hypotheses Tested	Adjusted Goodness-of-fit	Pr (>|χ^2|)	ΔAICc	K	Path	Path p-value	Path β-estimate	Endogenous Variable R^2	H_0 Outcome
H_{A1}, H_{A3}	0.61	0.02	22.41	10					Failure to Reject
H_{A2}, H_{A3}	0.50	< 0.01	17.87	7					Failure to Reject
H_{A2}, H_{A3}	0.75	0.12	9.38	7	Fall (Total) Discharge → Recruitment	0.72	-0.06	< 0.01	Failure to Reject
					NPGO → Recruitment	0.88	0.03		
					Winter PDO → Fall (Total) Discharge	0.07	-0.30	0.09	
H_{A1}, H_{A2}	0.48	< 0.01	26.52	11					Failure to Reject
H_{A1}, H_{A2}	0.49	< 0.01	26.08	11					Failure to Reject
H_{A1}, H_{A2}	0.50	0.01	25.99	11					Failure to Reject
H_{A1}, H_{A2}	0.52	0.01	24.74	11					Failure to Reject
H_{A1}, H_{A2}	0.49	< 0.01	26.59	11					Failure to Reject

Table 6 (continued)

Hypotheses Tested	Adjusted Goodness-of-fit	Pr (>|χ^2|)	ΔAICc	K	Path	Path p-value	Path β-estimate	Endogenous Variable R^2	H_0 Outcome
H_{A1}, H_{A2}	0.69	0.09	19.34	11	April (E GOA) Upwelling → Recruitment	0.54	-0.11	0.02	Failure to Reject
					Fall (Total) Discharge → Recruitment	0.66	-0.08		
					Winter NOI → April (E GOA) Upwelling	0.76	0.06	0.01	
					Winter PDO → April (E GOA) Upwelling	0.87	-0.03		
					Winter PDO → Fall (Total) Discharge	0.07	-0.30	0.09	
					Winter PDO ←→ Winter NOI	0.01	-0.54	NA	
H_{A1}, H_{A2}	0.67	0.07	19.90	11	May (E GOA) Upwelling → Recruitment	0.98	< 0.01	< 0.01	Failure to Reject
					Fall (Total) Discharge → Recruitment	0.73	-0.06		
					Winter NOI → May (E GOA) Upwelling	0.10	-0.33	0.10	
					Winter PDO → May (E GOA) Upwelling	0.88	-0.03		
					Winter PDO → Fall (Total) Discharge	0.07	-0.30	0.09	
					Winter PDO ←→ Winter NOI	0.01	-0.54	NA	

Table 6 (continued)

Hypotheses Tested	Adjusted Goodness-of-fit	Pr (>|χ^2|)	ΔAICc	K	Path	Path p-value	Path β-estimate	Endogenous Variable R^2	H_0 Outcome
H_{A1}, H_{A2}	0.76	0.20	17.23	11	June (E GOA) Upwelling → Recruitment	0.05	-0.33	0.12	Failure to Reject
					Fall (Total) Discharge → Recruitment	0.56	-0.10		
					Winter NOI → June (E GOA) Upwelling	0.14	-0.29	0.11	
					Winter PDO → June (E GOA) Upwelling	0.06	-0.37		
					Winter PDO → Fall (Total) Discharge	0.07	-0.30	0.09	
					Winter PDO ←→ Winter NOI	0.01	-0.54	NA	
H_{A1}, H_{A2}	0.73	0.14	18.21	11	Winter/Spring (W GOA) Upwelling → Recruitment	0.34	-0.16	0.03	Failure to Reject
					Fall (Total) Discharge → Recruitment	0.86	-0.03		
					Winter NOI → Winter/Spring (W GOA) Upwelling	0.03	0.38	0.28	
					Winter PDO → Winter/Spring (W GOA) Upwelling	0.23	-0.21		
					Winter PDO → Fall (Total) Discharge	0.07	-0.30	0.09	
					Winter PDO ←→ Winter NOI	0.01	-0.54	NA	

Table 6 (continued)

Hypotheses Tested	Adjusted Goodness-of-fit	Pr (>|χ^2|)	ΔAICc	K	Path	Path p-value	Path β-estimate	Endogenous Variable R^2	H_0 Outcome
H_{A1}, H_{A2}	0.74	0.15	17.89	11	June (W GOA) Upwelling → Recruitment	< 0.01	-0.60	0.37	Failure to Reject
					Fall (Total) Discharge → Recruitment	0.51	-0.09		
					Winter NOI → June (W GOA) Upwelling	0.25	-0.23	0.05	
					Winter PDO → June (W GOA) Upwelling	0.28	-0.22		
					Winter PDO → Fall (Total) Discharge	0.07	-0.31	0.09	
					Winter PDO ←→ Winter NOI	0.01	-0.54	NA	
H_{A1}	0.55	0.03	12.19	8					Failure to Reject
H_{A1}	0.55	0.03	12.23	8					Failure to Reject
H_{A1}	0.66	0.07	10.21	8	June (E GOA) Upwelling → Recruitment	0.05	-0.32	0.10	Failure to Reject
					Winter NOI → June (E GOA) Upwelling	0.14	-0.29	0.11	
					Winter PDO → June (E GOA) Upwelling	0.06	-0.37		
					Winter PDO ←→ Winter NOI	0.01	-0.54	NA	

Table 6 (continued)

Hypotheses Tested	Adjusted Goodness-of-fit	Pr (>|χ^2|)	ΔAICc	K	Path	Path p-value	Path β-estimate	Endogenous Variable R^2	H_0 Outcome
H_{A1}	0.58	0.03	11.69	8					Failure to Reject
H_{A1}	0.57	0.03	11.76	8					Failure to Reject
H_{A2}	-0.04	< 0.01	13.75	5					Failure to Reject
H_{A2}	0.48	0.02	6.39	5					Failure to Reject
H_{A3}	1.00	NA	0.00	3	NPGO → Recruitment	0.89	0.02	NA	Failure to Reject

Table 7 Pacific ocean perch analysis results (exploratory phase, age 0): Summary statistics from exploratory POP analysis examining conditions during age 0. Data are provided for the best SEM candidate models, sorted by ΔAICc relative to the model with the lowest AICc. Arrows point from exogenous to endogenous variables. K represents the number of parameters. Shaded cells indicate p-values ≤ 0.05

Adjusted Goodness-of-fit	Pr (>|χ^2|)	ΔAICc	K	Path	Path p-value	Path β-estimate	Endogenous Variable R^2
1.00	0.97	0.00	5	March (E GOA) Upwelling → Recruitment	0.98	< 0.01	< 0.01
				Winter NOI → March (E GOA) Upwelling	0.01	-0.42	0.18
1.00	0.91	0.01	5	May (W GOA) Upwelling → Recruitment	0.23	0.21	0.04
				NPGO → May (W GOA) Upwelling	0.88	0.03	< 0.01
1.00	0.89	0.02	5	July (W GOA) Upwelling → Recruitment	0.95	-0.01	< 0.01
				NPGO → July (W GOA) Upwelling	0.89	0.02	< 0.01
1.00	0.87	0.02	5	March (E GOA) Upwelling → Recruitment	0.98	< 0.01	< 0.01
				NPGO → March (E GOA) Upwelling	0.01	-0.42	0.18
1.00	0.85	0.03	5	June (E GOA) Upwelling → Recruitment	0.05	-0.32	0.10
				NPGO → June (E GOA) Upwelling	0.32	-0.17	0.03
0.99	0.83	0.05	5	June (E GOA) Upwelling → Recruitment	0.05	-0.32	0.10
				Winter NOI → June (E GOA) Upwelling	0.61	-0.09	0.01
0.97	0.63	0.23	5	Winter/Spring (W GOA) Upwelling → Recruitment	0.32	-0.17	0.03
				NPGO → Winter/Spring (W GOA) Upwelling	0.06	0.32	0.10
0.96	0.59	0.29	5	June (W GOA) Upwelling → Recruitment	< 0.01	-0.60	0.36
				Winter NOI → June (W GOA) Upwelling	0.51	-0.11	0.01
0.89	0.32	0.98	5	June (W GOA) Upwelling → Recruitment	< 0.01	-0.60	0.36
				NPGO → June (W GOA) Upwelling	0.12	-0.26	0.07

Table 8 Pacific ocean perch analysis results (exploratory phase, age 1): Summary statistics from exploratory POP analysis examining conditions during age 1. Data are provided for the best SEM candidate models, sorted by ΔAICc relative to the model with the lowest AICc. Arrows point from exogenous to endogenous variables. K represents the number of parameters. Shaded cells indicate p-values ≤ 0.05.

Adjusted Goodness-of-fit	Pr (>|χ^2|)	ΔAICc	K	Path	Path p-value	Path β-estimate	Endogenous Variable R^2
0.93	0.44	0.00	5	March (E GOA) Upwelling → Recruitment	0.51	-0.12	0.01
				Winter NOI → March (E GOA) Upwelling	0.01	-0.43	0.19
0.92	0.42	0.05	5	June (E GOA) Upwelling → Recruitment	< 0.01	-0.51	0.26
				Winter NOI → June (E GOA) Upwelling	0.57	-0.10	0.01
0.92	0.42	0.05	5	June (W GOA) Upwelling → Recruitment	0.04	-0.34	0.12
				Winter NOI → June (W GOA) Upwelling	0.51	-0.12	0.01
0.90	0.35	0.26	5	June (E GOA) Upwelling → Recruitment	< 0.01	-0.51	0.26
				Winter PDO → June (E GOA) Upwelling	0.18	-0.23	0.05
0.83	0.23	0.86	5	June (W GOA) Upwelling → Recruitment	0.04	-0.34	0.12
				NPGO → June (W GOA) Upwelling	0.11	-0.27	0.07
0.81	0.21	0.98	5	June (E GOA) Upwelling → Recruitment	< 0.01	-0.51	0.26
				NPGO → June (E GOA) Upwelling	0.27	-0.19	0.04
0.79	0.18	1.23	5	June (W GOA) Upwelling → Recruitment	0.04	-0.34	0.12
				Winter PDO → June (W GOA) Upwelling	0.58	-0.10	0.01
0.75	0.14	1.56	5	Late Spring (Total) Discharge → Recruitment	0.04	0.35	0.12
				Winter PDO → Late Spring (Total) Discharge	0.82	0.04	< 0.01
0.74	0.13	1.64	5	March (E GOA) Upwelling → Recruitment	0.51	-0.12	0.01
				NPGO → March (E GOA) Upwelling	< 0.01	-0.45	0.20

POP recruitment was unrelated to any environmental variables during age 2. Out of 49 models tested, 28 had insignificant χ^2 values and the two best models had similar AICc values and the same number of parameters (Table 9). Neither of these models showed any significant relationships between variables tested, and all coefficients of variation for recruitment were below 5%.

Discussion

All *a priori* hypotheses were rejected for both species, suggesting that the climate variables examined in this study do not relate to either species' recruitment through intermediary effects on larval advection. Sablefish recruitment was unrelated to the environmental factors that we used as indicators for variability in cross-shelf and along-shelf transport during age 0, suggesting that variability in larval advection towards nursery sites may not have a significant impact on their recruitment. POP recruitment was negatively related to upwelling-favorable winds during June, but none of the hypotheses tested were accepted in their entirety. Although one may expect surface-dwelling larvae to quickly reach the shelf in a downwelling system such as the GOA, this is not necessarily the case, in particular in the western GOA, where upwelling-favorable winds at the shelf break are common during spring and predominate after June (Fig. 7).

While we found little support for our *a priori* hypotheses, the exploratory analysis revealed some statistically significant relationships for both species that may reflect environmental influences on recruitment during juvenile stages, including a positive relationship between sablefish recruitment and July upwelling-favorable winds in the E GOA during age 1. The mechanism behind this relationship is unlikely to be related to advection, as sablefish reach their nursery sites well before this time period (Rutecki and Varosi, 1997a, b). Reduced

Table 9 Pacific ocean perch analysis results (exploratory phase, age 2): Summary statistics from exploratory POP analysis examining conditions during age 2. Data are provided for the best SEM candidate models, sorted by ΔAICc relative to the model with the lowest AICc. Arrows point from exogenous to endogenous variables. K represents the number of parameters.

Adjusted Goodness-of-fit	Pr (>|χ^2|)	ΔAICc	K	Path	Path p-value	Path β-estimate	Endogenous Variable R^2
1.00	0.96	0.00	5	April (E GOA) Discharge → Recruitment	0.81	-0.04	< 0.01
				Winter PDO → April (E GOA) Discharge	0.37	0.16	0.03
0.99	0.75	0.10	5	March (E GOA) Upwelling → Recruitment	0.27	-0.19	0.04
				Winter PDO → March (E GOA) Upwelling	0.13	0.27	0.07

downwelling in the summer may result in increased fall production along the E GOA coast (Waite and Mueter, 2013), which could benefit young sablefish in their coastal nursery grounds. Several studies documenting relationships between sablefish recruitment and upwelling attribute the relationship to food availability rather than advection (e.g., Schirripa and Colbert, 2006; Shotwell et al., 2014). McFarlane and Beamish (1992), examining recruitment of British Columbia sablefish, found that the Aleutian Low is positively associated with copepod abundance, southwesterly winter winds, and sablefish recruitment. They also found that sablefish diets in this region consist primarily of calanoid copepods, concluding that enhanced abundance of these prey is the likely mechanism behind these relationships (McFarlane and Beamish, 1992).

We found a positive relationship between our sablefish recruitment index and seasonal chlorophyll-*a* indices (Waite and Mueter 2013) for the western GOA shelf region during fall at age 1 during 1998 – 2009 ($r = 0.60$, $p = 0.04$). However, none of the chlorophyll-*a* indices were significantly correlated with July (E GOA) upwelling-favorable winds, suggesting that the relationship between sablefish recruitment and summer upwelling-favorable winds in the E GOA was unrelated to the relationship between summer upwelling and fall chlorophyll-*a* abundance found by Waite and Mueter (2013). This relationship may have been spurious or may have resulted from unknown mechanisms. However, the correlation between July (E GOA) upwelling-favorable winds and W GOA onshelf chlorophyll-*a*, while insignificant, did show the expected positive sign. Its insignificance may simply have been due to the limited length of the time series available for chlorophyll-*a*, resulting in low power for statistical tests of significance. Furthermore, while it is possible that the relationship between July (E GOA) upwelling-favorable winds and sablefish recruitment was spurious, its prevalence among the candidate models testing

relationships between recruitment and environmental conditions during age 1 suggests that a more in-depth examination of the relationship between July upwelling-favorable winds, summer and fall productivity, and sablefish recruitment is warranted, perhaps when a longer chlorophyll time series is available.

The sequential relationships between winter PDO, late winter/early spring freshwater discharge during ages 1 and 2, and sablefish recruitment may also have been due to productivity-related mechanisms. The intensified Aleutian Low associated with a positive PDO phase enhances onshore flow of moist air in the North Pacific (Cayan and Peterson, 1989; Trenberth, 1990; Trenberth and Hurrell, 1994; Mantua et al., 1997). This can lead to enhanced precipitation, earlier and enhanced water column stability, and earlier phytoplankton blooms during spring (Cayan and Peterson, 1989; Trenberth, 1990; Gargett, 1997; Weingartner et al., 2005; Henson, 2007). These early blooms tend to be more intense and shorter-lived, as they deplete nutrients more quickly than less intense blooms; furthermore, stronger water column stability throughout spring and summer can reduce primary and secondary productivity due to reduced mixing with nutrient-rich waters (Freeland et al., 1997; Eslinger et al., 2001; Henson, 2007). Because zooplankton reproduce more slowly than phytoplankton, this can result in underutilization of the intense, brief productivity associated with earlier blooms and reduced zooplankton biomass (Eslinger et al., 2001). Although the relationship between water column stability and primary productivity is more complex for the GOA shelf than for inner bays like Prince William Sound, both regions exhibit lower primary productivity during years with earlier, stronger, shallower stratification (Eslinger et al., 2001; Weingartner et al., 2005; Henson, 2007; Miller et al., 2012). It is plausible that these results indicate that a positive PDO phase, which corresponds to warmer temperatures and enhanced precipitation, leads to greater freshwater

discharge during late winter and early spring, and that this results in earlier water column stability, shorter, underutilized phytoplankton blooms, and reduced sablefish recruitment. Furthermore, the observation that freshwater discharge is related to recruitment at a slightly later lag during age 2 compared to age 1 is consistent with the observation that spring blooms typically occur later on the shelf than in enclosed coastal bays (Eslinger et al., 2001; Weingartner et al., 2005), and that age 2 is around when sablefish begin to leave coastal bays for shelf waters (Rutecki and Varosi, 1997b).

The observed negative relationship between POP recruitment and June upwelling-favorable winds in both the E GOA and W GOA during age 0 provides some support for our supposition that onshelf Ekman transport is conducive to POP recruitment, although it occurred after the period during which larval advection towards shore was hypothesized to occur. Our hypothesis was based on the timing of parturition, which occurs during April and May for POP. However, larval rockfish abundance on the shelf (not identified to species) has been observed to peak during summer (Doyle et al., 2009). Rockfish larvae found on the GOA shelf during July were similarly sized to those found over the slope and shelf during May, which suggests that the annual peak in rockfish larvae may be comprised of two cohorts: one that peaks during late spring and one during mid-summer, with POP likely associated with the earlier cohort (Miriam Doyle, University of Washington, Seattle, pers. comm.). This hypothesis is supported by recent genetic identification of rockfish larvae. Therefore, it is plausible that late spring is close to the peak time period for POP larvae reaching surface waters on the shelf. Moreover, Doyle et al. (2009) found a positive relationship between larval rockfish abundance on the shelf and optimal strength of alongshore winds during late spring. This may be analogous to the negative relationship between POP recruitment and June upwelling-favorable winds found in our analysis,

which may indicate that June is the time at which many POP reach the surface and that they are vulnerable at this time to advection towards or away from shore.

POP recruitment was also negatively related to June upwelling-favorable winds during age 1. While this may be indicative of a mechanism acting during both age 0 and age 1 but unrelated to larval advection, it may also reflect different mechanisms at different ages. Throughout much of the year, strong downwelling winds transport zooplankton from oceanic origins towards shore (Cooney, 1986, 1988). Shotwell et al. (2014), after linking sablefish recruitment to advection of oceanic properties associated with the North Pacific Polar Front, proposed a mechanism in which cool air from the Arctic enhances both primary and secondary production in central North Pacific waters, which are then advected onto the shelf during spring. Zooplankton and juvenile fish in Prince William Sound have exhibited offshore isotopic carbon signatures that vary interannually, indicating that planktivorous organisms in nearshore surface waters rely somewhat on a varying supply of productive waters from offshore that are likely transported to the shelf through onshore transport processes such as downwelling (Eslinger et al., 2001). It is possible that stronger downwelling-favorable winds at the slope may enhance advection of age 0 POP towards shore while simultaneously transporting waters abundant in phytoplankton and/or zooplankton, enhancing prey availability to age 1 POP already located close to shore.

Downwelling may also affect larval fish diets through an influence on zooplankton community composition rather than merely their abundance. Along the United States west coast, the greater downwelling of warm surface waters associated with a positive PDO phase leads to dominance of warm-water zooplankton taxa (Keister et al., 2011). These differ from cold-water zooplankton in size and fat content (Lee et al., 2006; Keister et al., 2011), which can have

important implications for fish diets (e.g., Trudel et al., 2002). The influence of onshore transport variability on zooplankton community composition is poorly understood for the GOA shelf, and may be pertinent to the relationship between downwelling and POP recruitment.

The observed positive relationship between POP recruitment and late spring (total) discharge may also be related to enhanced prey availability on the shelf. It is possible that higher discharge during late spring corresponds to longer winters, later stratification, and later spring blooms. In contrast with the dynamics of early spring blooms discussed earlier, years in which stratification occurs later in the year are associated with longer periods of weak water column stability accompanied by intermittent vertical mixing, longer phytoplankton blooms, and greater zooplankton productivity (Eslinger et al., 2001; Henson, 2007). This may enhance availability of the copepods and euphausiids that comprise the largest portion of juvenile POP diets (Carlson and Haight, 1976; Boldt and Rooper, 2009).

Given that their recruitment time series are uncorrelated ($r = -0.10$; $p = 0.58$) and show different degrees of interannual variability (Fig. 2), it may seem counterintuitive to investigate the same variables as potential mechanisms of both POP and sablefish recruitment. However, there are a number of scenarios in which species susceptible to similar mechanisms can exhibit different interannual patterns in their YCS. For instance, the influence of wind-induced transport on ichthyoplankton advection towards shore may differ according to their position in the water column, with deeper larvae being more susceptible to geostrophic flows and shallower ones to wind-driven flows (Lanksbury et al., 2007; Duffy-Anderson et al., 2013). Horizontal movement of Greenland halibut (*Reinhardtius hippoglossoides*) in the Bering Sea varies by depth, and is more variable at shallower depths (Duffy-Anderson et al., 2013). Similar dynamics have been observed in the GOA , where arrowtooth flounder (*Atheresthes stomias*) and Pacific halibut

(*Hippoglossus stenolepis*) larvae, which remain deeper (roughly 30 m) in the water column during their drift stage, exhibited more direct onshore movement than the surface-dwelling larvae of other flatfish species (Bailey et al., 2008). Although both POP and sablefish are believed to occupy near-surface waters during their drift phase, only sablefish are known to be neustonic (Kendall and Matarese, 1987; Wing and Kamikawa, 1995; Matarese et al., 2003). It is likely that, similar to the species examined in Bailey et al. (2008), sablefish exhibit less direct movement towards shore due to their shallower position in the water column. Additionally, some evidence suggests that sablefish undergo vertical migrations and are located deeper in the water column during the day (e.g., Wing and Kamikawa, 1995). Such behavior is not known in POP larvae. Differences in their vertical migration behavior may result in different responses to surface transport, which may require circulation models incorporating depth and behavior to more fully explore these concepts (Lanksbury et al., 2007).

Larvae can also be differentially affected by similar transport mechanisms if their spatial distributions differ (Lanksbury et al., 2007; Duffy-Anderson et al., 2013; Vestfals et al., 2013). For species that spawn in deep waters, location of spawning sites can strongly affect onshore movement. For example, spawning near cross-shelf canyons and gullies can allow eggs and larvae to take advantage of deep water transport along these features towards shore (Bailey et al., 2008). Onshelf flow at depth is associated with the downstream side of submarine canyons in the Bering Sea (Vestfals et al., 2013) and with the upstream side in the GOA (Stabeno et al., 2004). Flows can also vary among different canyons, potentially leading to variable relationships between onshore transport and recruitment of species whose eggs and larvae are located in different geographic areas (Duffy-Anderson et al., 2013; Vestfals et al., 2013). While specific spawning grounds are unknown for sablefish, POP are believed to release their larvae

near canyons at depth (Paraketsov, 1963; Gunderson, 1971; Rooper et al., 2007). If POP larvae are partially advected towards shore through canyons by deepwater currents prior to reaching the surface, the relationship between their recruitment and onshore surface transport may differ in timing or magnitude from that of sablefish.

Differences in other life history characteristics may also result in dissimilar recruitment patterns between two species that are susceptible to similar mechanistic influences on their recruitment. Species with slower larval development may require longer pelagic drift periods prior to settlement, and may fail to settle if they reach their nursery sites prematurely (Vestfals et al., 2013); therefore, years associated with faster advection towards nursery sites may not be similarly beneficial to two species with different rates of larval development. Different spawning or hatching times between two species may result in the same environmental factor becoming relevant at a different seasonal time period for each species, which can also contribute to differences in their recruitment time series. Precise drift timing is poorly understood for POP in the GOA, and may not be as similar to sablefish hatch timing as hypothesized in our *a priori* hypotheses.

Finally, multiple factors affect the recruitment of each species and differences in their relative importance can mask the effect of shared drivers that tend to synchronize recruitment between species. Recruitment of arrowtooth flounder, rock sole, and flathead sole in the Bering Sea were higher in years with enhanced onshelf flow, but other factors affected each species differently (Wilderbuer et al., 2002). Recruitment of English sole *(Parophrys vetulus)* off the Oregon and Washington coast is better explained by models incorporating temperature-mediated hatching success and successful wind-mediated advection to nursery sites compared to models only incorporating one or the other (Kruse and Tyler, 1989). Thus, while shared drivers can

result in synchronous recruitment between species, species-specific drivers can mask their effects and lead to different recruitment patterns.

This study further supports the idea that the shelves of the E and W GOA are subject to very different environmental influences. Both of our regional-scale variables exhibited different patterns of variability between the E GOA and areas further west. Freshwater discharge shows more interannual variability during winter and early spring in the E GOA and during fall in the C GOA (Fig. 12). This may help explain why neither species' recruitment was related to springtime indices of freshwater discharge in the C GOA; sablefish recruitment was related to E GOA discharge and both species' recruitments were related to total discharge. Because the total index is a measure of total discharge entering the Seward line from upstream, it is indicative of variation in freshwater discharge and the strength of the ACC in the W GOA (Royer, 1982; Royer and Grosch, 2006).

Downwelling patterns show a stark contrast between the E and W GOA, with the latter showing strong upwelling-favorable winds throughout much of the year, particularly during summer and fall, whereas the former exhibits a strong seasonal pattern with downwelling-favorable winds throughout most of the year. In light of these differences in variability, it is noteworthy that POP are related to late spring upwelling-favorable winds in both regions of the GOA while sablefish are related to summer upwelling-favorable winds in the E GOA only. This may reflect the higher density of young sablefish in the E GOA (Heifetz and Fujioka, 1991; Sigler et al., 2001; Maloney and Sigler, 2008), whereas juvenile POP are widely distributed throughout the northern GOA and Aleutian Islands (Rooper, 2008).

One of the concerns with this analysis is the use of SEM with relatively short time series that may have non-linear relationships. While SEM is a promising approach to testing

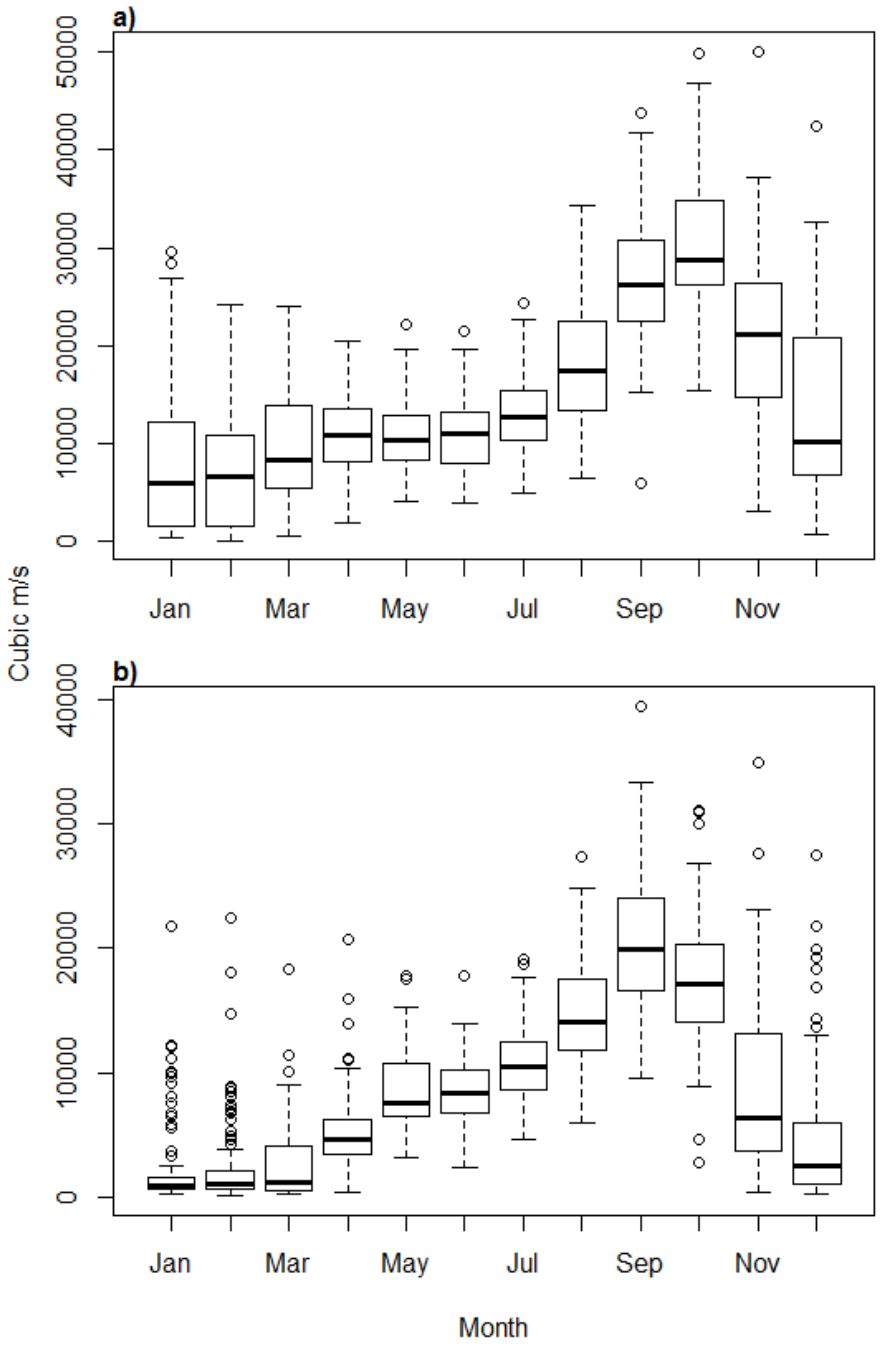

Figure 12. Seasonal freshwater discharge variability. Monthly freshwater discharge variability in (a) the eastern GOA and (b) the central GOA. Boxes encompass upper and lower quartiles; thick horizontal lines denote median values. Open circles denote outliers, defined as values lying beyond each quartile by a factor ≥ 1.5 times the interquartile range. Error bars mark the highest and lowest values excluding outliers.

relationships among large-scale climate drivers, regional environmental variability, and local or regional biological responses, several factors may limit the utility of SEM in this study. Firstly, SEM is based on linear regression and requires appropriate transformations, for example exponential terms, to evaluate nonlinear relationships (Bollen, 1989; Ullman et al., 2007). Since only linear relationships were hypothesized, it is possible that significant nonlinear relationships were overlooked. Secondly, SEM is a large-sample technique. Kline (1998) recommended a minimum sample size equal to ten times the number of parameters, which our larger models failed to meet, and all of our models failed to meet the sample sizes recommended by MacCallum et al. (1996), which range from 132 to 3,488 depending on the degrees of freedom.

Another complication in interpreting our results is the population structure of POP, which consists of numerous genetically distinct sub-populations throughout the GOA (Palof et al., 2011; Kamin et al., 2013). The authors hypothesize that this is not due to a sweepstakes effect, but to limited physical dispersal at all life stages. Thus, a gulfwide recruitment index for POP in the GOA may mask differences in local recruitment patterns and links between the gulfwide recruitment index and our environmental indices may be weak even if upwelling and discharge have local effects on some of the GOA POP subpopulations.

Finally, recruitment is a complex process susceptible to factors operating at multiple life stages (e.g., Kruse and Tyler, 1989; Wilderbuer et al., 2002). Here we focused on factors associated with larval drift and found no support for our *a priori* hypotheses, but exploratory analyses revealed relationships that may imply productivity-related mechanisms and may act during later life stages, such as during the return migration to adult habitat. Conversely, when more information on factors such as the locations of hatching and parturition becomes available, examining conditions prior to their larval drift period may also be informative.

Our results point to potential mechanisms warranting further investigation using more targeted process studies. We identified variables that may indicate advection and productivity-related mechanisms affecting recruitment of sablefish and POP, as well as the time periods during which these mechanisms may operate. Before these results can be applied in the management of these two species in the GOA, process studies would need to be conducted to confirm the proposed mechanisms.

The assessment model used to estimate sablefish and POP recruitment in the GOA, described previously, is capable of incorporating environmental time series as additional input (Wilderbuer et al., 2002; Maunder and Watters, 2003; Deriso et al., 2008; Hanselman et al., 2011a; Hanselman et al., 2011b). This allows managers to determine how recruitment is likely to deviate from the mean, given certain environmental conditions (Maunder and Watters, 2003). If the mechanisms behind the relationships found in our study are ascertained by further study, relevant variables could be incorporated into each species'assessment following, for example, the method outlined in Shotwell et al. (2014). They incorporated methodology from several other studies (Maunder and Watters, 2003; Francis, 2006; Deriso et al., 2008) to create the following approach, which rigorously evaluates an index's usefulness before its use in management:

First, an environmental time series (e.g., late winter E GOA discharge) is incorporated into the base model, creating an "environmental model" (Maunder and Watters, 2003):

$$R_t = \mu \exp(\alpha + \beta I_t + \varepsilon_t), \quad [3]$$

where R_t is the estimate of recruit abundance in year t; μ is the mean historical recruit abundance; β is a scaling parameter determing the magnitude of the relationship between the environmental index and recruitment; I_t is the environemtal index value in year t; ε_t refers to deviations in

recruitment; and α is a scaling parameter that removes bias from the environmental time series distribution (ensuring that μ remains equal to the recruitment mean) and is defined as follows:

$$\alpha = \ln\left(\frac{n}{\sum exp(\varepsilon_t + \beta I_t)}\right), \quad [4]$$

where *n* is the number of observations in the recruitment time series.

Next, multiple candidate indices (e.g., late winter and early spring discharge indices) are each incorporated into separate environmental models, and evaluated using a multi-stage hypothesis-testing procedure (Deriso et al., 2008), which rules out indices that are not useful. In this procedure, a χ^2 test is performed comparing each environmental model's negative log-likelihood to that of the base model, and those with insignificant differences from the base model are discarded (Deriso et al., 2008; Shotwell et al., 2014). Remaining models are then evaluated through randomization tests, in which the environmental index is randomly resampled many times and each re-sampling is used as an alternate index in its own environmental model. Differences in negative log-likelihoods are then compared among all of the resulting alternate environmental models; if the negative log-likelihood of the model using the observed index is within the first percentile of those using randomized indices, the index is considered important.

Prediction error is then assessed using cross-validation (Francis, 2006), in which remaining models are re-run several times, leaving out one year each time. That year is estimated based on the rest of the time series, and mean absolute error (MAE) is estimated as a measure of reliability in model predictions (Francis, 2006; Shotwell et al., 2014). Finally, the utility of remaining environmental models is evaluated using impact analysis, in which they are re-run with the environmental covariate held fixed and set to the average value for the environmental time series (Deriso et al., 2008; Shotwell et al., 2014). This helps determine what

the impact of fluctuations in the environmental covariate would be on variability in the recruitment estimates (Deriso et al., 2008; Shotwell et al., 2014).

If one of our environmental time series is evaluated using this procedure and shown to have significant use in predicting recruitment variability, an environmental model that includes it as a covariate can then be used to improve recruitment estimates in stock assessments. For predicting futures biomass trajectories, the assessment models for POP and sablefish use mean historical recruitments for the terminal year, and random draws from the statistical distribution of historical recruitments for future years (Hanselman et al., 2011a; Hanselman et al., 2011b). By incorporating pertinent environmental covariates, abundance of age 2 recruits can be estimated rather than randomly assigned for an additional three years, since the environmental data from the current year informs YCS two years into the future (Shotwell et al., 2014). This can reduce the uncertainty in recruitment projections, allowing for more accurate estimates of future biomass projections under alternate harvest scenarios and more accurate management reference points (Haddon, 2001; Maunder and Watters, 2003; Deriso et al., 2008; Hanselman et al., 2011a; Hanselman et al., 2011b; Shotwell et al., 2014).

While the mechanisms behind the relationships found in our study are uncertain, our methods and results may still be useful to researchers. More conclusive results, especially for our more complex models, can be obtained with a longer time series and with a more spatially explicit recruitment index for POP. Even if such an index is not developed, it would be beneficial to repeat this analysis in future years when longer time series are available for the variables used. In the meantime, our results provide information that may inform directed surveys investigating potential environment-recruit relationships, which may help improve recruitment estimates. It may be beneficial to analyze these relationships individually using

approaches that relax the linearity assumption, such as generalized additive models, until sample sizes are large enough to more reliably incorporate sequential causation into model structure using SEM.

Conclusions

The overall goal of this thesis was to investigate sequential relationships between climate variables, regional variables, and recruitment of sablefish and POP in the GOA, which I addressed through structural equation modeling using both hypothetis-testing and exploratory approaches. Based on these results, the answers to the questions asked in the introduction are as follows:

1. Is there a sequential relationship between winter PDO or NOI, spring downwelling-favorable winds in the GOA, and recruitment of sablefish or POP?

   No significant sequential relationship between these variables was found for either species. The structural models tested containing these relationships were either implausible, or they indicated that one or more of the relationships within the hypothesized sequence was insignificant.

2. Is there a sequential relationship between winter PDO, summer freshwater discharge in the GOA, and recruitment of sablefish or POP?

   Similar to the first question, no significant sequential relationship between these variables was found for either species.

3. Is POP recruitment negatively related to the NPGO?

   No. In all models containing a path between NPGO and POP recruitment, that path was not found to be significant.

While these questions were met with negative answers, the analysis did yield some interesting results. For example, the significant relationships that sablefish recruitment shares with July upwelling-favorable winds and late winter/early spring freshwater discharge warrant further inquiry, as they may indicate relationships between meteorological forces, productivity, and recruitment which may be of interest to managers in the future. Furthermore, the relationship between POP recruitment and June upwelling-favorable winds indicates a strong possibility that the advection of larval POP towards shore, and their subseuent recruitment, is sensitive to variability in downwelling strength.

There are several factors that would have been useful to address if more time and resources had been available, some of which may clarify the mechanisms behind relationships that were found. While I investigated chlorophyll-*a* concentration as a potential explanation for some relationships, the underlying motivation for using this index was the assumption that it reflects conditions leading directly to increased production of copepods and euphausiids, the main components of both species' diets during their early life history (Carlson and Haight, 1976; McFarlane and Beamish, 1992; Sigler et al., 2001; Boldt and Rooper, 2009). A spatially and seasonally explicit time series of zooplankton abundance would have been more useful for determining whether downwelling and freshwater discharge affect each species' recruitment through effects on production of their prey.

Predation on larval sablefish and POP, while poorly understood, may also have been informative to address in this study. Sablefish larvae have been found in black-legged kittiwake diets at interannually variable levels (Hatch, 2013), though Kendall and Matarese (1987) suggest that sablefish are relatively effective at avoiding predation. Potential predators of larval POP include common murres (*Uria aalge*), Pacific cod, Pacific halibut, and arrowtooth flounder

(Ainley et al., 1993; Rooper et al., 2007). With a better understanding of each species' main predators, and with time series of each predator's relative abundance, interannual variability in predation pressure on larval sablefish and POP could have been accounted for as a potential confounding variable. Additionally, better information on the locations of eggs and larval hatching/parturition, as well as factors that may influence fecundity and hatching success, may have improved the explanatory power of our analyes (e.g., Kruse and Tyler, 1989; Vestfals et al., 2013).

Meso-scale eddies were not addressed because long time series of eddy kinetic energy are currently unavailable. However, eddies can be an important mechanism for increased cross-shelf exchange and productivity, and their net effects on larval fish advection can vary; depending on their position relative to larval fish, they may transport them closer to or farther from suitable habitats (Janout et al., 2009; Ladd et al., 2009; Atwood et al., 2010). The behavior of eddies in the GOA across years may have been useful to include as a potential driver of variability in larval sablefish and POP advection towards shore.

Some of the variables that were used had multiple representative indices available, which could have been used to corroborate the results. The NOI is negatively correlated with the El Niño-Southern Oscillation (ENSO), but was chosen for this analysis because it is believed to be more directly related to conditions in the North Pacific (Schwing et al., 2002). However, some studies have found that ENSO events are related to recruitment of other groundfish species in the GOA, and proposed mechanisms include enhanced onshore advection of their larvae (e.g., Bailey and Picquelle, 2002). The ENSO index could have been used in place of, or in addition to, the NOI index as a potential reflection of conditions driving downwelling variability in the GOA. Furthermore, while the downwelling index downloaded from PFEL serves as an acceptable

measure of onshore transport, their organization also offers indices of derived surface wind and ocean transport vectors (PFEL, 2011). These could have been used in additional models as alternate measurements of onshore surface water transport. Finally, the Resource Ecology and Fisheries Management Divison at the Alaska Fishies Science Center has developed the Ocean Surface Current Simulator (OSCURS), which models surface water transport over time throughout the North Pacific and has been used to model larval drift patterns of species such as walleye pollock (Ingraham, 1997). Using OSCURS, it may have been informative to plant virtual particles along the shelf break throughout the hypothesized larval drift periods for sablefish and POP, and to note the rate at which particles reach the nearshore. This could have been done for each year throughout the range of each species' recruitment time series, and the data used as an index of onshore advection success. Particle tracking models, including OSCURS and similar others, have been used in numerous studies to test and corroborate relationships between transport-related mechanisms and fish recruitment (Wilderbuer et al., 2002; Lanksbury et al., 2007; Keister et al., 2011; Duffy-Anderson et al., 2013; Vestfals et al., 2013). Such an approach would likely have been useful here.

Despite these concerns, we believe that this study is potentially useful to other studies, as well as to the goals of the GOA IERP. The approach used here may be useful to studies examining environment-recruit relationships wherein multiple sequential mechanisms are hypothesized. Many studies examining relationships between large-scale climate features and fish recruitment imply indirect mechanisms involving one or more intermediate variables (e.g., King et al., 2001; Bailey and Picquelle, 2002). SEM is a useful technique for testing whether such mechanistic assumptions are consistent with the observed data's covariance structure, and can be used either as an exploratory or as a corroborative analysis phase.

In addition, studies using environmental variables that contain significant spatial or temporal variability can use hierarchical cluster analysis to identify and select the most pertinent regions and lags to use in their analysis. This enables the use of temporal and spatial scales that are appropriate for each variable when performing statistical analyses, which helps avoid issues with redundancy or collinearity. For each of our variables, we were able to identify times of the year that show coherent interannual patterns of variability, which can be used to isolate seasonal lags for use in time series analyses. We were also able to identify a spatial pattern in downwelling variability that highlights differences between the E and W GOA. These patterns can be particularly useful to the GOA IERP, one of the goals of which is to quantify timing and importance of oceanographic mechanisms controlling ocean conditions in the E and W GOA, with the hypothesis that the mechanisms determining juvenile survival differ between these two regions (NPRB, 2011). Characterizing seasons and spatial regions in oceanographic features that display coherent patterns of variability across years is a crucial step towards identifying oceanographic mechanisms that work on regional scales.

Our results may also contribute to the GOA IERP goal to build a system of models describing connections among climate, oceanography, productivity, and early life survival of the project's five focal species (NPRB, 2011). We found that POP recruitment may be enhanced by strong downwelling-favorable winds during their larval drift period, and that recruitment of both species may be related to wind and freshwater discharge-mediated variability in primary and secondary productivity on the shelf during their early life history. If targeted process studies verify that these are the mechanisms reflected by our results, this can have substantial implications for management and for the GOA IERP. These environmental indices could be incorporated into each species' stock assessment model, allowing for greater confidence and

accuracy in future harvest projections and management reference points (Haddon, 2001; Maunder and Watters, 2003; Deriso et al., 2008; Shotwell et al., 2014). Furthermore, confirming these mechanisms would contribute valuable information to linkages among climate, oceanography, productivity, and early life survival that the GOA IERP aims to understand (NPRB, 2011).

While our results do not confirm these mechanisms, they do contribute valuable information on areas where further study would be most useful. There are a number of efforts being made under the GOA IERP that can contribute greater certainty to our results. Studies on physical and biological mechanisms that influence spatial and temporal patterns in primary and secondary productivity, including analysis of satellite-derived chlorophyll-*a* concentration, can help clarify any potential linkages between freshwater discharge during early and late spring and primary productivity on the GOA shelf (NPRB, 2011). Data on zooplankton are being collected along the Seward Line, which can help inform interannual variations in their abundance and community composition (NPRB, 2011). If collected along more spatially explicit transects, this can also contribute insight into temporal and regional variability in production of sablefish and POP prey items, which can also be valuable in testing proposed mechanisms between oceanography, prey productivity, and recruitment of these two species.

Other projects and efforts under the GOA IERP include the deployment of satellite-tracked drifters that are used to examine ocean transport, annual surveys of egg, zooplankton, and larval fish abundance and distribution, and analyses of habitat associations to create habitat suitability maps for each species (NPRB, 2011). With longer time series, each of these can improve certainty in our results. Egg and larval fish data will allow us to identify interannual variability in timing, origins, and progression of these two species during their drift period.

Habitat studies will allow us to identify their potential nearshore nursery habitat with greater precision. Model-derived transport indices could then be used to model fish progression from better known hatch sites to better known nursery sites (e.g., Wilderbuer et al., 2002; Duffy-Anderson et al., 2013), and these models could be corroborated with data on larval progression from annual samples and statistically compared to the environmental indices used in this study.

In conclusion, it is unlikely that the PDO, NOI, or NPGO significantly influence larval advection of GOA sablefish or POP to nursery sites through variability in downwelling-favorable winds and freshwater discharge. However, years with above average downwelling-favorable winds during June had stronger year-classes of POP, indicating that downwelling-favorable winds may enhance recruitment of POP larvae through increased onshore transport. Moreover, downwelling-favorable winds and freshwater discharge during the juvenile stage (age 1 and 2) showed some significant relationships with the recruitment of both species, which may be due to variability in primary and secondary productivity associated with meteorological and oceanographic conditions reflected by these indices. These putative relationships will need to be corroborated by additional evidence from process studies to better elucidate the mechanisms affecting survival of juvenile sablefish and POP, and ongoing efforts under the GOA IERP may contribute valuable information towards achieving that goal.

References

Ainley, D.G., Sydeman, W.J., Parrish, R.H., Lenarz, W.H., 1993. Oceanic factors influencing distribution of young rockfish (*Sebastes*) in central California- a predator's perspective. Calif. Coop. Ocean. Fish. Invest. Rep. 34, 133-139.

Allen, M.J., Smith, G.B., 1988. Atlas and zoogeography of common fishes in the Bering Sea and northeastern Pacific. U.S. Department of Commerce, NOAA Tech. Rept. NMFS 66, 151 pp.

Atwood, E., Duffy-Anderson, J.T., Horne, J.K., Ladd, C., 2010. Influence of mesoscale eddies on ichthyoplankton assemblages in the Gulf of Alaska. Fish. Oceanogr. 19, 493-507.

Bailey, K.M., Abookire, A.A., Duffy-Anderson, J.T., 2008. Ocean transport paths for the early life history stages of offshore-spawning flatfishes: a case study in the Gulf of Alaska. Fish. Fish. 9, 44-66.

Bailey, K.M., Picquelle, S.J., 2002. Larval distribution of offshore spawning flatfish in the Gulf of Alaska: potential transport pathways and enhanced onshore transport during ENSO events. Mar. Ecol. Prog. Ser. 236, 205-217.

Boldt, J.L., Rooper, C.N., 2009. Abundance, condition, and diet of juvenile Pacific ocean perch (*Sebastes alutus*) in the Aleutian Islands. Fish. Bull. 107, 278-285.

Bollen, K.A., 1989. Structural equations with latent variables. John Wiley & Sons, Inc, New York, New York, USA.

Bollen, K.A., 2002. Latent variables in psychology and the social sciences. Annu. Rev. Psychol. 53, 605-634.

Bond, N.A., Overland, J.E., Spillane, M., Stabeno, P., 2003. Recent shifts in the state of the North Pacific. Geophys. Res. Lett. 30, 2183-2186.

Burnham, K.P., Anderson, D.R., 2002. Model selection and milti-model inference: a practical information-theoretic approach. Springer Science + Business Media, Inc., New York, New York, USA.

Carlson, H.R., Haight, R.E., 1976. Juvenile life of Pacific ocean perch, *Sebastes alutus*, in coastal fjords of southeastern Alaska: their environment, growth, food habits, and schooling behavior. T. Am. Fish. Soc. 105, 191-201.

Carlson, H.R., Straty, R.R., 1981. Habitat and nursery grounds of Pacific rockfish, *Sebastes* spp., in rocky coastal areas of southeastern Alaska. Mar. Fish. Rev. 43, 13-19.

Cayan, D.R., Peterson, D.H., 1989. The influence of North Pacific atmospheric circulation on streamflow in the West, in: Peterson, D.H. (Ed.), Aspects of Climate Variability in the Pacific and the Western Americas. AGU, Washington, DC, USA, pp. 375-397.

Chhak, K.C., Di Lorenzo, E., Schneider, N., Cummins, P.F., 2009. Forcing of Low-Frequency Ocean Variability in the Northeast Pacific. J. Climate 22, 1255-1276.

Cooney, R.T., 1986. The seasonal occurrence of *Neocalanus cristatus*, *Neocalanus plumchrus*, and *Eucalanus bungii* over the shelf of the northern Gulf of Alaska. Cont. Shelf Res. 5, 541-553.

Cooney, R.T., 1988. Distribution and ecology of zooplankton in the Gulf of Alaska: a synopsis. Bull. Ocean Res. Inst. Univ. Tokyo 261, 27-41.

Deriso, R.B., Maundeer, M.N., Pearson, W.H., 2008. Incorporating covariates into fisheries stock assessment models with application to Pacific herring. Ecol. Appl. 18, 1270-1286.

Di Lorenzo, E., Combes, V., Keister, J.E., Strub, P.T., Thomas, A.C., Franks, P.J.S., Ohman, M.D., Furtado, J.C., Bracco, A., Bograd, S.J., Peterson, W.T., Schwing, F.B., Chiba, S., Taguchi, B., Hormazabal, S., Parada, C., 2013. Synthesis of Pacific Ocean climate and ecosystem dynamics. Oceanography 26, 68-81, http://dx.doi.org/10.5670/oceanog.2013.76.

Di Lorenzo, E., Schneider, N., Cobb, K.M., Franks, P.J.S., Chhak, K., Miller, A.J., McWilliams, J.C., Bograd, S.J., Arango, H., Curchitser, E., Powell, T.M., Rivière, P., 2008. North Pacific Gyre Oscillation links ocean climate and ecosystem change. Geophys. Res. Lett. 35, L08607.

Doyle, M.J., Picquelle, S.J., Mier, K.L., Spillane, M.C., Bond, N.A., 2009. Larval fish abundance and physical forcing in the Gulf of Alaska, 1981-2003. Prog. Oceanogr. 80, 163-187.

Duffy-Anderson, J.T., Blood, D.M., Cheng, W., Ciannelli, L., Matarese, A.C., Sohn, D., Vance, T.C., Vestfals, C., 2013. Combining field observations and modeling approaches to examine Greenland halibut (*Reinhardtius hippoglossoides*) early life ecology in the southeastern Bering Sea. J. Sea Res. 75, 96-109.

Eslinger, D.L., Cooney, R.T., McRoy, C.P., Ward, A., Kline, T.C., Simpson, E.P., Wang, J., Allen, J.R., 2001. Plankton dynamics: observed and modelled responses to physical conditions in Prince William Sound, Alaska. Fish. Oceanogr. 10, 81-96.

Fissel, B., Dalton, M., Felthoven, R., Garber-Yonts, B., Haynie, A., Himes-Cornell, A., Kaspersi, S., Lee, J., Lew, D., Pfeiffer, L., Sepez, J., Seung, C., 2012. Economic status of the groundfish fisheries off Alaska, 2011. Stock Assessment and Fishery Evaluation Report for the Groundfish Fisheries of the Gulf of Alaska and Bering Sea/Aleutian Islands Area, North Pacific Fishery Management Council, 605 W. 4th Ave, Suite 306 Anchorage, AK 99501, 309 pp.

Fox, J., 2006. Structural equation modeling with the sem package in R. Struct. Equ. Modeling 13, 465-486.

Francis, R.I.C.C., 2006. Measuring the strength of environment–recruitment relationships: the importance of including predictor screening within cross-validations. ICES J. Mar. Sci. 63, 594-599.

Freeland, H., Denman, K., Wong, C.S., Whitney, F., Jacques, R., 1997. Evidence of change in the winter mixed layer in the Northeast Pacific Ocean. Deep-Sea Res. Pt. I 44, 2117-2129.

Fukuwaka, M.A., Kaga, T., Azumaya, T., 2011. Regional differences in climate factors controlling chum and pink salmon abundance. ICES J. Mar. Sci. 68, 1131-1137.

Gargett, A.E., 1997. The optimal stability `window': a mechanism underlying decadal fluctuations in North Pacific salmon stocks? Fish. Oceanogr. 6, 109-117.

Grace, J.B., Anderson, T.M., Olff, H., Scheiner, S.M., 2010. On the specification of structural equation models for ecological systems. Ecol. Monogr. 80, 67-87.

Gunderson, D.R., 1971. Reproductive patterns of Pacific ocean perch (*Sebastes alutus*) off Washington and British Columbia and their relation to bathymetric distribution and seasonal abundance. J. Fish. Res. Board Can. 28, 417-425.

Gunderson, D.R., 1972. Evidence that Pacific ocean perch (*Sebastes alutus*) in Queen Charlotte Sound form aggregations that have different biological characteristics. J. Fish. Res. Board Can. 29, 1061-1070.

Gunderson, D.R., 1977. Population biology of Pacific ocean perch, *Sebastes alutus*, stocks in the Washington-Queen Charlotte Sound region, and their response to fishing. Fish. Bull. 75, 369-403.

Haddon, M., 2001. Modelling and quantitative methods in fisheries. Chapman & Hall/CRC, Boca Raton, Florida, USA.

Hanselman, D.H., Lunsford, C.R., Rodgveller, C.J., 2011a. Assessment of the sablefish stock in Alaska. Stock Assessment and Fishery Evaluation Report for the Groundfish Resources of the Gulf of Alaska, North Pacific Fishery Management Council, 605 W 4th Ave, Suite 306 Anchorage, AK 99501, 307-412.

Hanselman, D.H., Shotwell, S.K., Hulson, P., Heifetz, J., Ianelli, J., 2011b. Assessment of the Pacific ocean perch stock in the Gulf of Alaska. Stock Assessment and Fishery Evaluation Report for the Groundfish Resources of the Gulf of Alaska, North Pacific Fishery Management Council, 605 W. 4th Ave, Suite 306 Anchorage, AK 99501, 821-892.

Hare, S.R., Mantua, N.J., 2000. Empirical evidence for north Pacific regime shifts in 1977 and 1989. Prog. Oceanogr. 47, 103-145.

Hatch, S.A., 2013. Kittiwake diets and chick production signal a 2008 regime shift in the northeast Pacific. Mar. Ecol. Prog. Ser. 477, 271-284.

Heifetz, J., Fujioka, J.T., 1991. Movement dynamics of tagged sablefish in the northeastern Pacific. Fish. Res. 11, 355-374.

Henson, S.A., 2007. Water column stability and spring bloom dynamics in the Gulf of Alaska. J. Mar. Res. 65, 715-736.

Hollowed, A.B., Wooster, W.S., 1992. Variability of winter ocean conditions and strong year classes of northeast Pacific groundfish. ICES Mar. Sc. 195, 433-444.

Ingraham, W.J., 1997. Getting to know OSCURS, REFM's ocean surface current simulator. AFSC Research Activities: Quarterly Report for April-May-June 1997, 1-14.

Janout, M.A., Weingartner, T.J., Okkonen, S.R., Whitledge, T.E., Musgrave, D.L., 2009. Some characteristics of Yakutat eddies propagating along the continental slope of the northern Gulf of Alaska. Deep-Sea Res. II 56, 2444-2459.

Kamin, L.M., Palof, K.J., Heifetz, J., Gharrett, A.J., 2013. Interannual and spatial variation in the population genetic composition of young-of-the-year Pacific ocean perch (*Sebastes alutus*) in the Gulf of Alaska. Fish. Oceanogr. 23, 1-17.

Keister, J.E., Di Lorenzo, E., Morgan, C.A., Combes, V., Peterson, W.T., 2011. Zooplankton species composition is linked to ocean transport in the Northern California Current. Glob. Change Biol. 17, 2498-2511.

Kendall, A.W., Matarese, A.C., 1987. Biology of eggs, larvae, and epipelagic juveniles of sablefish, *Anoplopoma fimbria*, in relation to their potential use in management. Mar. Fish. Rev. 49, 1-13.

Kimura, D.K., Shimada, A.M., Shaw, F.R., 1998. Stock structure and movement of tagged sablefish, *Anoplopoma fimbria*, in offshore northeast Pacific waters and the effects of El Niño Southern Oscillation on migration and growth. Fish. Bull. 96, 462-481.

King, J.R., McFarlane, G.A., Beamish, R.J., 2000. Decadal-scale patterns in the relative year class success of sablefish (*Anoplopoma fimbria*). Fish. Oceanogr. 9, 62-70.

King, J.R., McFarlane, G.A., Beamish, R.J., 2001. Incorporating the dynamics of marine systems into the stock assessment and management of sablefish. Prog. Oceanogr. 49, 619-639.

Kline, R.B., 1998. Principles and practice of structural equation modeling. Guilford Press, New York, New York, USA.

Kruse, G.H., Tyler, A.V., 1989. Exploratory simulation of English sole recruitment mechanisms. T. Am. Fish. Soc. 118, 101-118.

Ladd, C., Crawford, W.R., Harpold, C.E., Johnson, W.K., Kachel, N.B., Stabeno, P.J., Whitney, F., 2009. A synoptic survey of young mesoscale eddies in the Eastern Gulf of Alaska. Deep-Sea Res. II 56, 2460-2473.

Lanksbury, J.A., Duffy-Anderson, J.T., Mier, K.L., Busby, M.S., Stabeno, P.J., 2007. Distribution and transport patterns of northern rock sole, *Lepidopsetta polyxystra*, larvae in the southeastern Bering Sea. Prog. Oceanogr. 72, 39-62.

Lee, R.F., Hagen, W., Kattner, G., 2006. Lipid storage in marine zooplankton. Mar. Ecol. Prog. Ser. 307, 273-306.

MacCallum, R.C., Browne, M.W., Sugawara, H.M., 1996. Power analysis and determination of sample size for covariance structure modeling. Psychol. Methods 1, 130-149.

Maloney, N.E., Sigler, M.F., 2008. Age-specific movement patterns of sablefish (*Anoplopoma fimbria*) in Alaska. Fish. Bull. 106, 305-316.

Mantua, N.J., Hare, S.R., Zhang, Y., Wallace, J.M., Francis, R.C., 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bull. Amer. Meteorol. Soc. 78, 1069-1079.

Mason, J.C., Beamish, R.J., McFarlane, G.A., 1983. Sexual maturity, fecundity, and early life-history of sablefish (*Anoplopoma-fimbria*) off the Pacific coast of Canada. Can. J. Fish. Aquat. Sci. 40, 2126-2134.

Matarese, A.C., Blood, D.M., Picquelle, S.J., Benson, J.L., 2003. Atlas of abundance and distribution patterns of ichthyoplankton from the northeaset Pacific Ocean and Bering Sea ecosystems based on research conducted by the Alaska Fisheries Science Center (1972 - 1996). NOAA Professional Paper NMFS 1, 281p.

Maunder, M., Watters, G., 2003. A general framework for integrating environmental time series into stock assessment models: model description, simulation testing, and example. Fish. Bull. 101, 89-99.

McFarlane, G.A., Beamish, R.J., 1992. Climatic influence linking copepod production with strong year-classes in sablefish, *Anoplopoma fimbria*. Can. J. Fish. Aquat. Sci. 49, 743-753.

Miller, S.E., Adkison, M.D., Haldorson, L., 2012. Relationship of water column stability to the growth, condition, and survival of pink salmon (*Oncorhynchus gorbuscha*) in the northern coastal Gulf of Alaska and Prince William Sound. Can. J. Fish. Aquat. Sci. 69, 955-969.

Mueter, F.J., Pyper, B.J., Peterman, R.M., 2005. Relationships between coastal ocean conditions and survival rates of northeast Pacific salmon at multiple lags. T. Am. Fish. Soc. 134, 105 - 119.

NPRB (North Pacific Research Board), 2011. Gulf of Alaska project. Accessed 10 October, 2013: http://gulfofalaska.nprb.org/

Palof, K.J., Heifetz, J., Gharrett, A.J., 2011. Geographic structure in Alaskan Pacific ocean perch (*Sebastes alutus*) indicates limited lifetime dispersal. Mar. Biol. 158, 779-792.

Paraketsov, I.A., 1963. On the biology of *Sebastodes alutus* of the Bering Sea, in: Moiseev, P.A. (Ed.), Soviet Fisheries Investigations in the Northeastern Pacific, Part I, available from US Department of Commerce, Natl. Tech. Inf. Serv., Springfield, VA, pp. 319-327. As TT67-51203.

PFEL (Pacific Fisheries Environmental Laboratory), 2011. Upwelling and environmental index products. Accessed 15 September, 2011: http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/PFELindices.html

R Development Core Team, 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org

Rodionov, S.N., Overland, J.E., Bond, N.A., 2005. The Aleutian Low and Winter Climatic Conditions in the Bering Sea. Part I: Classification. J. Climate 18, 160-177.

Rooper, C.N., 2008. An ecological analysis of rockfish (*Sebastes* spp.) assemblages in the North Pacific Ocean along broad-scale environmental gradients. Fish. Bull. 106, 1-11.

Rooper, C.N., Boldt, J.L., Zimmermann, M., 2007. An assessment of juvenile Pacific ocean perch (*Sebastes alutus*) habitat use in a deepwater nursery. Estuar. Coast. Shelf S. 75, 371-380.

Royer, T.C., 1982. Coastal fresh-water discharge in the northeast Pacific. J. Geophys. Res.-Oc. Atm. 87, 2017-2021.

Royer, T.C., Grosch, C.E., 2006. Update of a freshwater discharge model for the Gulf of Alaska, North Pacific Research Board Final Report 734, 12 pp.

Rutecki, T.L., Varosi, E.R., 1997a. Distribution, age, and growth of juvenile sablefish, *Anoplopoma fimbria*, in Southeast Alaska, In: Wilkins, M.E., Saunders, M.W. (Eds.). Biology and Management of Sablefish. NOAA Tech. Rept. NMFS 130, pp 45 - 54.

Rutecki, T.L., Varosi, E.R., 1997b. Migrations of juvenile sablefish, *Anoplopoma fimbria*, in Southeast Alaska, In: Wilkins, M.E., Saunders, M.W. (Eds.). Biology and Management of Sablefish. NOAA Tech. Rept. NMFS 130, pp 123 - 130.

Salmon, D.K., 1992. On interannual variability and climate change in the North Pacific. PhD Thesis, University of Alaska Fairbanks, USA, 219 pp.

Sasaki, T., 1985. Studies on the sablefish resources of the North Pacific Ocean. Bull. Far Seas Fish. Res. Lab. (Shimizu) 22, 1 - 108.

Schirripa, M.J., Colbert, J.J., 2006. Interannual changes in sablefish (*Anoplopoma fimbria*) recruitment in relation to oceanographic conditions within the California Current system. Fish. Oceanogr. 15, 25-36.

Schneider, N., Cornuelle, B.D., 2005. The Forcing of the Pacific Decadal Oscillation. J. Climate 18, 4355-4373.

Schwing, F.B., Murphree, T., Green, P.M., 2002. The Northern Oscillation Index (NOI): a new climate index for the northeast Pacific. Prog. Oceanogr. 53, 115-139.

Shotwell, S.K., Hanselman, D.H., Belkin, I.M., 2014. Toward biophysical synergy: investigating advection along the Polar Front to identify factors influencing Alaska sablefish recruitment. Deep-Sea Res. II, http://dx.doi.org/10.1016/j.dsr2.2012.08.024.

Sigler, M.F., Rutecki, T.L., Courtney, D.L., Karinen, J.F., Yang, M.-S., 2001. Young of the year sablefish abundance, growth, and diet in the Gulf of Alaska. Alsk. Fish. Res. Bull. 8, 57-70.

Sogard, S.M., 2011. Interannual variability in growth rates of early juvenile sablefish and the role of environmental factors. Bull. Mar. Sci. 87, 857-872.

Stabeno, P.J., Bond, N.A., Hermann, A.J., Kachel, N.B., Mordy, C.W., Overland, J.E., 2004. Meteorology and oceanography of the northern Gulf of Alaska. Cont. Shelf Res. 24, 859-897.

Trenberth, K.E., 1990. Recent observed interdecadal climate changes in the Northern Hemisphere. Bull. Amer. Meteorol. Soc. 71, 988-993.

Trenberth, K.E., Hurrell, J.W., 1994. Decadal atmosphere-ocean variations in the Pacific. Clim. Dyn. 9, 303-319.

Trudel, M., Tucker, S., Zamon, J.E., Morris, J.F.T., Higgs, D.A., Welch, D.W., 2002. Bioenergetic response of coho salmon to climate change. NPAFC Tech. Rept. No. 4. 59-61.

Ullman, J.B., Tabachnick, B.G., Fidell, L.S., 2007. Structural equation modeling, in: Hartman, S. (Ed.), Using multivariate statistics, Fifth Edition ed. Pearson Education, Inc, Boston, Massachusetts, USA, pp. 676 - 780.

Vestfals, C.D., Ciannelli, L., Duffy-Anderson, J.T., Ladd, C., 2013. Effects of seasonal and interannual variability in along-shelf and cross-shelf transport on groundfish recruitment in the eastern Bering Sea. Deep-Sea Res. II, http://dx.doi.org/10.1016/j.dsr1012.2013.1009.1026.

Waite, J.N., Mueter, F.J., 2013. Spatial and temporal variability of chlorophyll-*a* concentrations in the coastal Gulf of Alaska, 1998–2011, using cloud-free reconstructions of SeaWiFS and MODIS-Aqua data. Prog. Oceanogr. 116, 179-192.

Ward, J.H., 1963. Hierarchical grouping to optimize an objective function. J. Am. Stat. Assoc. 58, 236 - 244.

Weingartner, T., 2007. The physical environment of the Gulf of Alaska, in: Spies, R. (Ed.), Long-term ecological change in the northern Gulf of Alaska. Elsevier, Amsterdam, pp. 12-47.

Weingartner, T., Coyle, K.O., Finney, B., Hopcroft, R.R., Whitledge, T., Brodeur, R., Dagg, M.J., Farley, E., Haidvogel, D.B., Haldorson, L., Hermann, A.J., Hinckley, S., Napp, J.M., Stabeno, P., Kline, T., Lee, C.M., Lessard, E., Royer, T.C., Strom, S.L., 2002. The northeast Pacific GLOBEC program: coastal Gulf of Alaska. Oceanography 15, 48-63.

Weingartner, T., Eisner, L., Eckert, G.L., Danielson, S., 2009. Southeast Alaska: oceanographic habitats and linkages. J. Biogeogr. 36, 387-400.

Weingartner, T.J., Danielson, S.L., Royer, T.C., 2005. Freshwater variability and predictability in the Alaska Coastal Current. Deep-Sea Res. II 52, 169-191.

Wilderbuer, T.K., Hollowed, A.B., Ingraham Jr, W.J., Spencer, P.D., Conners, M.E., Bond, N.A., Walters, G.E., 2002. Flatfish recruitment response to decadal climatic variability and ocean conditions in the eastern Bering Sea. Prog. Oceanogr. 55, 235-247.

Wing, B.L., 1997. Distribution of sablefish, *Anoplopoma fimbria*, larvae in the eastern Gulf of Alaska: neuston-net tows versus oblique tows, In: Wilkins, M.E., Saunders, M.W. (Eds.). Biology and Management of Sablefish. NOAA Tech. Rept. NMFS 130, pp 13 - 25.

Wing, B.L., Kamikawa, D.J., 1995. Distribution of neustonic sablefish larvae and associated ichthyoplankton in the eastern Gulf of Alaska, May 1990. NOAA Tech. Memo. NMFS-AFSC-53, 54 p.

Wolotira, R.J., Sample, T.M., Noel, S.F., Iten, C.R., 1993. Geographic and bathymetric distributions for many commercially important fishes and shellfishes off the west coast of North America, based on research survey and commercial catch data, 1912-84, U.S. Department of Commerce, NOAA Tech. Memo. NMFS-AFSC-6, 184 pp.